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A CHRONOSEQUENCE  
OF SOILS AND VEGETATION  
NEAR THE  
FRANZ JOSEF GLACIER.

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A thesis  
submitted in partial fulfilment  
of the requirements for the Degree  
of  
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in the  
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by  
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Lincoln College

1963



Oblique aerial photograph of Franz Josef Glacier looking south; showing Waiho River, terraces, roches moutonnées and access road. December, 1961.

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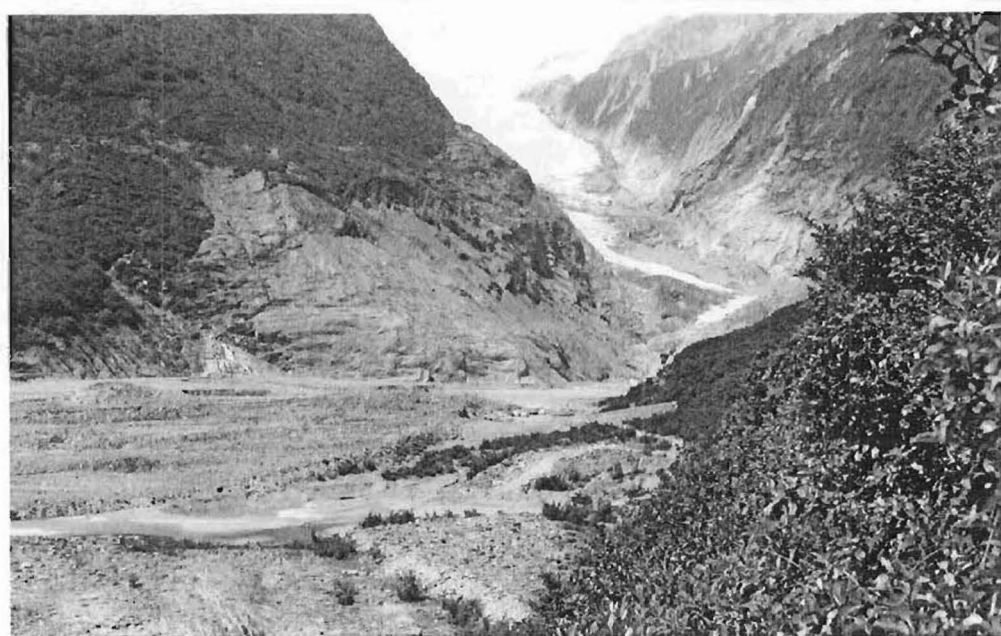
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The Franz Josef in Retreat.

## I.

INTRODUCTION

The recent rapid retreat of the Franz Josef Glacier in South Westland has produced extensive tracts of morainic debris, subsequently fashioned into a series of terraces of varying ages by the meandering Waiho River. These bare and boulder-strewn terraces have been colonised by a succession of different plant communities, and examination of the area by botanists led to the recognition of [six representative stages in this succession, whose ages could be accurately determined.]

[A sequence of very youthful soils has developed on the parent material concomitantly with these successive colonisation stages, and is initiated and influenced mainly by the various plant communities following each other.] The major feature of soil development is the progressive accumulation of organic matter in the upper few centimetres of mineral material, and on the surface as a deep, fibrous, greasy brown mor, interlaced with actively ramifying roots.

The situation therefore presents a classical opportunity to investigate a 'Chronosequence' of soils (and associated vegetation), because the youthful sequence of soils within this restricted area have developed under uniform climate on level topography from identical parent materials at 'time zero'. Soil differences are thus due to the lapse of different increments of time since the terraces were formed and plant succession was initiated.

In this juvenile stage of soil development the gradual accumulation of organic matter governs changes in many soil

properties. Therefore, the total amounts of organic matter and the proportions of its various constituents are of paramount importance. Accordingly, it was thought profitable to attempt measurement of only some changes in soil properties, lack of time precluding a more extensive investigation. In spite of sampling problems presented by the unusually coarse parent material, it was hoped that the changes in pH, amounts of Carbon, Nitrogen and organic Phosphorus in the mineral soil, the mor layer and in the vegetation would be interesting and would elucidate the initial processes of soil development. Three earlier studies in Alaska and California on similar situations provided some details of the processes concerned, but it was hoped to extend and refine in various ways the methods used by these workers. The investigations at Franz Josef in all their facets are recorded in the following pages, and it is thought that they may represent a useful addition to the state of knowledge in this field.

## II.

REVIEW OF LITERATURE

## II. 1. STUDIES ON SOIL DEVELOPMENT AND PLANT SUCCESSION.

## II. 1 (1) THE CHRONOFUNCTION.

A Chronosequence is a sequence of soils (and associated vegetation) whose differences are primarily due to differences in their ages, the other soil forming factors being held 'constant' or ineffectively varying. If the Fundamental Equation of Soil Forming Factors

$s = f(cl, o, r, p, t....)$  (Jenny; 1941, 1946, 1958, 1961) is evaluated for Time a Chronofunction is expressed as

$$s = f(\text{time})_{cl, o, r, p...}$$

that is; the magnitude of any soil property (s) is related to Time, if the subscripts climate, biotic factor, relief and parent material are constant or ineffectively varying. Jenny insisted that the soil forming factors act independently, and that the extent of soil development be measured with reference to a 'time zero'. In practice, this restricts Chronosequence studies to monogenetic soils, where development has occurred during a definite period on a virgin PM. Time is an anomolous soil forming factor, having no influence of itself, but governing the influences of the other factors on the soil until an apparent dynamic steady-state is achieved. The further development of Jenny's ideas can be seen in the series of papers published in 1946, 1958, 1960 and 1961, and in Harradine

and Jenny (1958), which re-inforce and extend the original theory. In 1958 he illustrated sequences and functions of the soil forming factors with large hypothetical models of Ecosystems, and later (1961) considered the Ecosystem per se and derived State Factor Equations based on the fluxes and potentials of matter and energy through its arbitrary boundaries. Thus Ecosystem properties are a function of the three State Factors:

1. The assemblage of properties at Time Zero (PM, relief)
2. The external flux potentials (Climate and biotic factor)
- and 3. The age of the Ecosystem.

The implications and ramifications of Jenny's theories have been discussed at length by Major (1951) and Crocker (1952, 1959), together with several other authors, notably Stephens (1947, 1951). Crocker is critical of the concept 'time zero', as any inter-dependence and inconstancy of the other four soil forming factors leads to the interruption and diversion of soil development, and a new time zero must be taken. As variations (e.g. of climate) are slow, there is "an elusively migratory time zero". Again, this virtually confines investigations to monogenetic soils, where the PM is "the initial state of the soil system at time zero" (Jenny, 1941), and is a fresh deposit such as glacial moraine, catastrophic volcanic deposition or river alluvium. This is the most important criticism of Jenny's concepts. Crocker also dealt at length with problems of soil and plant evolution and succession, concluding that polygenesis is the rule in soil development, excepting the restricted cases outlined above. The greatest contribution of Major and Crocker lies in their helpful elucidation of the biotic factor and the

concept of soil and plant co- evolution, related to the time sequence of events determined by the particular levels of climate, organisms, relief and PM obtaining in an Ecosystem.

Stephens has criticised Jenny largely on mechanistic grounds, stating that the functions are mathematically naive, and that substitution in them is inherently impossible due to the difficulty of assessing numerical values of the soil forming factors. He also objected (1947) to the independence of the factors, and attempted to derive further equations allowing dependent and independent factors to be considered. The only truly independent soil forming factor, according to Stephens, is Time. The integration

$$s = \int f(cl, o, r, w, p) dt \quad (\text{where } \underline{w} \text{ is "water table"})$$
 is preferred.

An excellent discussion on determining time scales of natural objects has been made by Zeuner (1958); and the time dimension has recently been used in pedological survey by the recognition of 'groundsurfaces' formed by successive 'interruptions' due to 'perturbations' such as climatic change or erosion; the groundsurface (persistent zone) being not significantly altered during the "K cycle" between interruptions (Butler, 1956; Butler and Hutton, 1956; Ward, 1958). Molloy (pers. comm.) has recently identified successive groundsurfaces in the Waimakariri Valley. Pollen analysis and the time factor in pedogenesis have been covered by Barrett (1961).

## II. 1 (2) SOME SOIL/PLANT ECOLOGICAL STUDIES.

It is intended here to review briefly some of the soil studies made in connection with successional development of plant associations. The treatise by Handley (1954) deals fully with aspects of organic matter (OM) accumulation in forest soils, and Wright (1949) has dealt basically with the broad role of biotic surveys in soil studies. Cooper and Rudolph (1953) considered evidence pertaining to the initiation of soil formation by lichens.

Quantitative correlations between vegetation changes and soil development have been reviewed by Billings (1941), with an extended treatment in another paper (1952). He has discussed a number of interesting papers, some of which can be briefly mentioned, as they contain notes on the different approaches to soil development experiments. Braun-Blanquet and Jenny (1926) studied the progressive podzolisation of a raw limestone soil (pH 7.2 - 7.6) by climate and a succession of vegetation from a calciphilous Firmetum (Carex firma) to an acidophilous Curvuletum (Carex curvula). The podzolising effect of different plants was also noted by Lipmaa (1940) in Estonia, and by Chandler (1938). The edaphic effects of various pines and hardwoods have been reported by Fisher (1928), Griffith et al (1930) and Gast (1937). The grasslands of Western North Dakota were studied by Hanson and Whitman (1938), and the invasion by forest by abandoned grass and cropland initiated soil changes discussed by Judd and Weldon (1939). Further



studies of interest were undertaken by Davis (1940) on mangroves, and by Cowles (1899) on the sand dunes of Lake Michigan.

Successional changes of soils on sand-dunes under different plant associations have been fruitful fields for study. The Chronosequences reported by Salisbury (1925), Burges and Drover (1953) and Cowie (1962) will be fully reviewed later, and are improvements on edapho-ecological investigations such as those by Olsen (1958) at Lake Michigan, Willis et al (1959) at Braunton Burrows and Barrett (1962) at Seaton Sluice. These papers showed the gradual accumulation of OM, differentiation of horizons, loss of bases and decreasing %BS under sand-dune pioneers such as Carex spp. and Ammophila arenaria, together with the eventual dominant scrub and forest communities. Barrett emphasised microfloral and microfaunal effects on OM, while Olsen established interesting connections between the composition of the PM and dominant climax species.

Chronosequences of soils and vegetation on recessional glacial moraines (Crocker and Major, 1955; Crocker and Dickson, 1957) will be fully reviewed in the next section (II. 1 (3)), but there are also a number of papers dealing principally with the plant ecology of glacial moraines which contain occasional references to soil development. These are more properly covered in the last Chapter of this Review of Literature (II. 4 (1)).

Some miscellaneous papers on soil/plant co-development may

now be mentioned briefly. Ike and Stone (1958) investigated soil N accumulation under black locust, a leguminous tree. Soils under locust trees contained the equivalent of approximately 600 lb N/ac/20" depth more than the adjacent and unforested soils, but there were no significant differences in pH, OM, bulk density and 'easily extracted' K and P between these areas. Mackney (1961) has reported at length on a podzol development sequence under oakwoods and heath in England, tracing the translocation of clay and iron and eluviation of humus, resulting in podzol intergrades, iron podzols and eventually humus-iron podzols. Many associated chemical data are presented. A similar study was undertaken by Coile (1940) using loblolly pine invasions of abandoned agricultural land. He reported an increased depth of the A<sub>0</sub> horizon, increased organic C and C/N ratios (stable N levels) and decreased infiltration and percolation rates despite virtually unchanged volume-weight, water-holding capacity and pore-space. The investigation also elucidated some features of competition involved in this invasion by loblolly pine, and eventual dominance of other species such as oak and hickory. Wilde et al (1954) have given useful details on methods of survey whilst studying some relationships between soils and forest growth in Canada. In New Zealand, Atkinson (1959) has followed soil changes under Pinus radiata. Another interesting study is that of Gorham (1953a), where topography produced two dissimilar soils (a flushed mulloid Brown Earth under ash and sycamore; a leached podzolic moroid Brown Earth under oak

and birch) with the same PM and climate during equal periods of time. Similarly, Gorham (1953b) demonstrated the production of topogenous and ombrogenous peats, showing increase of acidity and decrease of %BS and levels of N in a sequence from a relatively inorganic lake bed to a raised bog.

## II. 1 (3) CHRONOSEQUENCES.

There are not many reports of Chronosequence studies in the relevant literature, and only one review of the topic. Consequently, this section will deal at some length with eleven papers published since the review by Jenny (1941) (p. 32 et seq). Some attention has already been given in this Review of Literature to work connecting soil and plant development, but which has failed to stress adequately the Time factor.

Jenny's review covered work done to 1941, some of which was rather unsophisticated scientifically. Hilger, Geikie, Goodchild and Hirschwald attempted to demonstrate differential weathering of various rocks; the work of Hardy and van Baren on volcanic deposits was reported; and also that of Schreckenthal and Hoffman on the moraines of the Mittelburg Glacier. Tamm, Mattson and Lonnemark, and Aaltonen studied rates of podzolisation in Swedish soils. The San Joaquin soil family in California gave Shaw a good illustration of a Chronosequence. There are two other Chronosequences reported by Jenny which deserve special mention: dune sequences at Blakeney Point and Southport (Salisbury, 1925), and development of polder soils after reclamation (Hissink, 1938). Both situations showed great

similarity in soil development: progressive leaching of carbonates and decrease of pH, increase in OM content, decrease in %BS and total bases, development of structure and differentiation of horizons, and a floral succession from calcicole to calcifuge species. In both cases carbonate content fell to zero in approximately 300 years (from 9.4% in the polder and 6.3% at Southport), but the rate of loss differed due to the initial drainage difficulties of the  $\text{Na}^+$ -saturated, de-flocculated clay polder.

Chandler (1942) studied the process of podzolisation on glacial moraines in Alaska, but neglected to keep PM constant and mistakenly assumed constant volume-weight figures for soils and litters. Some results are presented below:

Table 1.. Some soil characteristics in an Alaskan Chronosequence.

<u>Age</u> (yrs)	<u>Total amt. OM</u> in $A_0$ and 0-8" of mineral soil. (lb/ac)	<u>pH. Surface 2"</u>
15	15,959	5.37
90	89,480	5.05
250	455,704	4.32
<u>+1000</u>	874,143	3.67

From mechanical analysis and morphological examinations he concluded that podzol development had not proceeded very far in 1000 years.

Next, Hutton (1950) combined time and PM differences of a 170 mile transect through loess-derived soils in South-West Iowa into a "Chrono-litho-sequence", attempting to keep vegetation, climate, micro-organisms and relief constant. Progressing away from the source of loessial material he found greater proportions of clay and lesser proportions of sand, and the depth of the soil decreased. Due to the rare intermittent depositions of loess at the distal end of the transect Hutton thought that the soils there would be older, and presented a graph of sand content and depth of soil against a time base and showed that the effect of PM is most important in soils of the first 60 miles of the transect (lithosequence), whereas from 60 to 170 miles Time determined degree of soil development (Chronosequence). The extreme difficulty of ensuring constancy of the other soil forming factors casts doubt on this ingenious but restricted approach.

Burges and Drover (1953) investigated a series of parallel sand dunes initiated by the drop in sea-level approximately 4000 years ago. A transect 4500 yards long was drawn radially through the dunes and a time scale of 1 yard=1 year assumed. This is probably not justified, but the sequence of soils and vegetation was clear. The soils developed from dune sands to iron podzols and eventually (beyond 3000 yards) to humus podzols; correlating closely with the vegetation sequence (1) dune colonisers, (2) Eucalyptus botryoides, Angophora intermedia and (3) Angophora lanceolata. The course of soil

development resembles that reported by Salisbury. In 50 years half the  $\text{CaCO}_3$  had been leached, in 200 years it had all gone from the upper solum, and the pH dropped from 8.8 to 6.0. From 200 to 2000 years an iron podzol gradually developed with stratification of OM and iron in distinct horizons, and the surface soil pH dropped to 5.5. After 3000 years an abrupt change to humus podzols occurred (surface pH 4.5), and was directly correlated with individuals of A. lanceolata. Few chemical data are presented.

Further studies on sand-dune soil development, with a more satisfactory emphasis on the redistribution of nutrients within the Ecosystem than previously reported, have been made by Wright (1955, 1956) at Culbin Forest. Several interesting effects of Corsican Pine on the sand-dunes were demonstrated, including the obvious features of dune stabilisation and OM accumulation. Firstly, data are presented showing the low natural fertility of sand, and the importance of grain size on total P, available P and available K. The low levels of P directly restrict the ultimate levels of OM from forest growth and litter return. Secondly, the counteraction of leaching by the organic cycle is treated with reference to the age of the forest trees. In young trees (less than 22 years old) removal of nutrients (especially Ca, K) from the soil exceeds return, in spite of a large leaf-fall. After 20-25 years the canopy closes and the trees mature, and nutrients are removed from lower horizons of the solum, the return and subsequent leaching of the litter replenishing the meagre nutrient stock. The

nutrient content of litter tends to depend, within broad limits, on the species of tree rather than the soil. Sodium, not required for plant growth, is leached from the upper solum. Wright and Will (1958) then gave very detailed data on nutrient content of trees and their components, showing how these change with maturity, and stressing the importance of litter return and root removal in the nutrient balance of a young but relatively infertile soil. These data greatly improve our knowledge of soil development on sand-dunes. The preliminary work of Cowie (1962) on sand-dunes in New Zealand has confirmed features of the other studies. He showed the same changes in soils with increasing age: increase in OM content, development of the B horizon with a greater proportion of finer mineral fractions and progressive leaching, leading to decrease of %BS (from 100% to 30%), and pH (from 9 to 6) in 7000 years. Four distinct dune-building stages were recognised: less than 100 years, less than 600-700, 1700 to 3000, and 7000 years ago.

Three classical Chronosequence studies have been made by Crocker, Dickson and Major in Alaska and California. In each case, accurate dating of the surfaces upon which soils and plants developed enabled precise measurement of nutrient accumulation rates, and some constancy of the other four soil forming factors was achieved. These papers (Dickson and Crocker, 1953-1954, at Mount Shasta; Crocker and Major, 1955, at Glacier Bay; Crocker and Dickson, 1957, at the Herbert and Mendenhall Glaciers) may be discussed, compared and contrasted together. At Mt. Shasta (warmer but drier than in Alaska) the

oldest soil of the sequence was 1200+ years, compared with about 200 years at Glacier Bay and Herbert/Mendenhall. Sampling sites were closely connected with the plant succession, which is more fully described in a later section of this Review. The Mt. Shasta succession included the N-fixers Alnus spp. and Ceanothus spp. (proven N-fixer; Bond, 1958a), with Purshia tridentata (probable N-fixer; T.M.Morrison, pers. comm.), and the climax community was dominated by Pinus ponderosa. The moraine successions included the N-fixers Dryas Drummondii, Alnus spp. and (at Herbert/Mendenhall) Lupinus nootkanensis, with an abrupt transition at 60-70 years to a spruce-cottonwood community, sub-climaxing at 100 years with spruce, and eventually two species of Hemlock after 200-300 years. As retreat of the Herbert/Mendenhall Glaciers was slower than at Glacier Bay, colonisation occurred sooner after retreat. Marked changes in bulk density were reported, in all three areas from 1.4+ to 0.8 in the upper 2" of mineral soil. This is closely related to the increasing organic C which, in approximately 200 years, reached 9 kg/m<sup>2</sup> at Mendenhall, 7 kg/m<sup>2</sup> at Herbert and 5 kg/m<sup>2</sup> at Glacier Bay. These values reflect the climatic differences between these areas, as PM's were very similar. Total soil organic C reached a steady-state after about 400 years at Mt. Shasta. The accumulation of total soil N is most interesting. In 60 years, 3360 lb/ac had accumulated at Mt. Shasta, compared with 2760 lb/ac in 50 years at Glacier Bay and 1800 lb/ac in 60 years at Herbert/Mendenhall. However, after the alder/spruce transition at Glacier Bay, total N dropped markedly



to less than  $200 \text{ g/m}^2$  (1920 lb/ac) at 188 years, whereas a gradual increase continued after the transition at Herbert/Mendenhall. The higher accumulation rate recorded at Glacier Bay is probably a result of the pits being chosen on finer material, and the decrease of total soil N is probably due to translocation to the aerial portions of the trees. C/N ratios widened as soil development progressed, but these did not increase as much at Mt. Shasta as in the glacial areas. Reaction of soils and litters became more acid during the sequences, with the F/H layers being most acid, except at Mt. Shasta, where the recent litter was most acid. A feature common to all three sequences was the negligible degree of mineral weathering, and the lack of horizon differentiation, except by OM accumulation. This contrasts with Chandler's data, but he investigated older soils. The studies at Glacier Bay and Herbert/Mendenhall have not revealed juvenile or incipient podzolisation. Base exchange data at Mt. Shasta showed a close dependence on OM, with increased CEC but loss of bases and decreased %BS. The top few inches of the oldest soils at Mt. Shasta had exchange capacities of approximately 50 me.% and %BS of much less than 50, especially in the oldest soil. The operation of the organic cycle was clearly demonstrated.

Lastly, the recent work of Tezuka (1961) in Japan on the slow succession from 'petridesert' (Reynoutria, Carex spp.) to scrub (Alnus sieboldiana), thence to a mixed deciduous-evergreen forest with an evergreen climax (Shiia sieboldiana, Machilis thunbergii) showed similarities in soil development to Mt. Shasta. Changes in bulk density were recorded, though pH did not change

significantly. Maximum total soil N ( $0.8\%$ ;  $990 \text{ g/m}^2$ ) was reached in less than 1000 years; a much higher level of N than at Mt. Shasta or in Alaska. Rainwater may have contributed  $7.5 \text{ kg/ha}$  of N per annum. The rate of increase of OM was about  $250 \text{ kg/ha/annum}$ , only half that recorded at Glacier Bay. Further data were presented, but in general the treatment of the Chronosequence was not as satisfactory as the classical work described above. Aspects of theoretical plant ecology were discussed at length, and little emphasis laid on the soil characteristics. Unfortunately the value of an excellent situation was not fully exploited.

From this material it is possible to draw some general conclusions regarding Chronosequence studies:

1. The difficulty of ensuring strict constancy of the other soil forming factors over the whole sequence is noted, and the consequent necessity to restrict the area of study. Some markedly different results, attributed to climate and PM, were noted even between the Herbert and Mendenhall Glaciers, and these differences become vital when comparing different areas.
2. It is essential to sample the whole Ecosystem, rather than only mineral soil and forest floor. Translocations of nutrients from soil to tree and back to litter layers may thus be traced.
3. It is extremely difficult to sample these bouldery soils. Sampling methods on a volume-weight basis must be

developed to suit the conditions on moraines, and to ensure that the Ecosystem is adequately sampled. Properly randomised sampling and a satisfactory statistical basis for experimentation seems virtually impossible. The selection of areas with abnormally high proportions of fine material or boulders may lead to anomolous results.

4. Permanent steady-states of dynamic equilibria of nutrient accumulation and removal are generally not achieved in short-period studies such as these, although at Mt. Shasta there were indications of transient steady-states of total N and C levels in the soil after 400 years. There are different rates of attainment of equilibrium by each soil component, and in these studies mineralogical weathering and horizon differentiation had hardly started.

5. The course of soil development is directly and completely correlated with the advent and growth of various communities of vegetation. There is a dependence on the areal pattern of plant distribution, with certain species having distinctive and specific effects. In this connection, the rate of accumulation of N depends upon the introduction, growth and disappearance of sub-pioneers such as Alnus, Dryas, Purshia and Ceanothus, which are related ecologically to external factors (location and state of neighbouring Ecosystems, pre-adaption of disseminules, accidents of dispersal), and to the effects of the dominant successional associations, through varying tolerance of the competition for light, nutrients and water.

## II. 1 (4) THE ROLE OF PHOSPHORUS IN VEGETATIONAL SUCCESSION AND ORGANIC MATTER ACCUMULATION.

We have seen that the major feature of soil development in the early phases of Chronosequences is the accumulation of OM, and it is instructive to review briefly some factors governing this accumulation. Factors affecting the P content of OM have recently been reviewed by Barrow (1961), drawing on the work of Walker (1956) and others, who considered the accumulation of OM in grassland soils. This early work led to three papers describing studies on OM (Walker and Adams, 1958, 1959; Walker, Thapa and Adams, 1959), all of which have been well reviewed and extended by Ludecke (1962) and Floate (1962). Walker (1962) considered problems of soil fertility in a grass/animal regime, and used his earlier hypotheses to elucidate soil forming processes in relation to nutrient deficiencies. Briefly, the theory of OM formation proposed by Walker is this: the presence of finely comminuted virgin PM at time zero is assumed (river alluvium, glacial till), and plant succession commences. As the N content of virgin mineral matter is very low, legumes (or non-leguminous N-fixers) will be the only species of higher plants able to grow. These utilise stocks of inorganic P and convert it to organic P in the OM, which contains mostly C, H, O, N, S and P, all of which (except P) may generally be obtained from the atmosphere and water. OM is incorporated into the soil and mineralisation of N and P proceeds. Grasses and other non-leguminous non-N-fixing plants may now establish, and these compete strongly for P

(Mouat and Walker, 1959a+b). When only the least soluble and positionally unavailable forms of inorganic P remain, N-fixers are unable to get their requirements in competition with non-N-fixers for the meagre amounts of mineralised P, and so are eliminated. N fixation virtually ceases and C/N ratios of OM widen.

Although S deficiency may limit growth of N-fixers in some areas, the P content of the PM governs the ultimate levels of OM in the soil in the absence of fertiliser P, the effect being most marked under conditions of moderate weathering and leaching (Walker and Adams, 1958). This study revealed wide variations in P contents of PM's throughout a "Lithosequence" of New Zealand soils. This was then extended to a study of weathering and leaching effects on a uniform PM (greywacke), and showed the decrease of total P and decrease of %inorganic P with increase of %organic P described above, over a wide range of weathering and leaching, inducing vegetational changes towards species less demanding of soil nutrients. The third study (Walker et al, (1959) exemplified these ideas in a "Chronosequence" of agricultural soils developed from pumice-land with the application of super-phosphate.

The ecological implications of these hypotheses have been covered by Beadle (1949, 1953, 1954, 1962a), dealing principally with soil P and the delimitation of plant communities. These papers represent welcome attention by ecologists to the edaphic factor in plant succession. A feature of the Chronosequences

previously described has been the lack of appreciation of the importance of N-fixers in colonising associations (priseres) on virgin PM's. A good review of N in natural plant communities was presented by Coaldrake (1962).

The very obvious increases in soil N, and the growing realisation of the importance of non-leguminous N-fixation, will be fully reviewed in the next section. Beadle demonstrated marked dependence of floristic composition on soil P content, but Coaldrake and Haydock (1958) have disagreed with his findings. The generally low P content of Australian soils has been discussed by Ozanne et al (1961) and Beadle (1962b).

Lastly, the forms of soil P and their distribution in profiles and particle-size fractions have been covered by Williams and Saunders (1956a+b) and Scheffer et al (1960). Sands contain little organic P and total P, and their inorganic P is largely in the form of primary phosphates (Ca-P). On the other hand, clays and silts contain more P than sands, with high proportions of organic P and secondary phosphates (Fe and Al-P).

## II. 2. THE ACCUMULATION OF NITROGEN IN SOILS.

### II. 2 (1) INTRODUCTION.

The place of N in plant ecology and herbage production has recently been reviewed by Walker (1954, 1956) and Tezuka (1958). Beadle and Tchan (1955) have dealt with semi-arid plant communities in Australia. More specifically, the N cycle in grassland soils has been covered by Richardson (1938) and Walker (1956c). Butler and Bathurst (1956) have discussed the transference of N from legume to grass, an important link in the N cycle. Lastly, the enigma of soil N balance sheets has been described by Allison (1955), showing the serious discrepancies which still exist in our knowledge of the N cycle.

Many aspects of N in tropical soils, which are equally applicable to temperate regions, have been very adequately reviewed by several authors in a publication by the CSIRO Committee of the Division of Tropical Pastures (1962). It is worthwhile tabulating the various sources of N for soils, some of which will be discussed further:

1. PM minerals.
2. Air, via rainwater.
3. Symbiotic N fixation.
  - a. Legumes.
  - b. Non-legumes.
  - c. Leaf-gland symbioses.
  - d. Lichens and liverworts.
4. Asymbiotic N fixation.
  - a. Heterotrophic bacteria.
  - b. Photosynthetic bacteria.
  - c. Autotrophic bacteria.
  - d. Fungi and yeasts.
  - e. Algae.

5. Non-biological fixation.
  - a. Photochemical fixation.
  - b. Surface adsorption from air.
6. Fertilisers, manures, feeds and seeds.

The remaining sections will deal more fully with

1. Aerial deposition of N.
2. Asymbiotic N fixation.
3. Symbiotic N fixation, with emphasis on the non-legumes.

## II. 2 (2) AERIAL DEPOSITION OF NITROGEN.

Eriksson (1952, 1958) has adequately reviewed the topic. Broadly speaking, he found total N in rain to be highest in the Northern Hemisphere (averaging 7.2 lb/ac/annum in Europe) and low in the tropics, though the proportion of  $\text{NO}_3\text{-N}$  was highest there. Virtanen (1952) and Eriksson have cast doubt on the widely held supposition that N fixation by thunderstorms is significant. Ingham (1950a+b) has supposedly demonstrated the adsorption of staggering amounts of N by soil organic colloids, extending the ideas of Liebig. While it is difficult to find exact experimental evidence to refute these data, his theory cannot be reconciled with agronomic experience on infertile soils. Wilson (1959a+b) reported on the forms of N in New Zealand snows and postulated mechanisms for their production. At 7000' on the Tasman Glacier (25 miles from the sea) he collected snow containing minute traces of  $\text{NO}_3\text{-N}$  and  $\text{NO}_2\text{-N}$ , 0.1 ppm  $\text{NH}_4\text{-N}$  and 0.12 ppm albuminoid-N. Slightly larger amounts of N could probably be expected in rain water at Franz Josef (A.T. Wilson; pers.comm.). At Lincoln, Gray (1888)



recorded only 6.4 ppm total N (1.87 lb/ac/annum) in 22 inches of rain. Miller (1906) at Rothamsted recorded 3.8 lb/ac/annum, with a maximum of 4.4 lb/ac/annum; but Crowther and Ruston (1911) analysed rainwater in an industrial area and recorded 8 to 18 lb/ac/annum of N, nearly all as  $\text{NH}_4\text{-N}$ . The variability of N deposition from rainwater over the United States was discussed by Junge (1958), who could find no close correlation of deposition with any physical or human feature except regional soil type. Lastly, Miller (1961) at Taita found less than 3 lb/ac/annum of N in rainwater, mostly organic (albuminoid). From this evidence it appears that additions of N to soils by rainwater are of a low order, although they may be significant over long periods of time if the N is rapidly utilised and not leached.

## II. 2 (3) ASYMBIOTIC FIXATION.

This topic has been reviewed by Jensen (1950) and P.W. Wilson (1958), but a few additional pertinent facts might be mentioned here. Possible heterotrophic N-fixing bacteria include Azotobacter spp., Beijerinckia spp. and Clostridium spp. The evidence relating to the ubiquity and activity of Azotobacter is conflicting, but in general fixation is thought to be small or negligible. Tchan and Beadle (1955) considered that the maximum possible contribution of Azotobacter in most habitats would not be greater than 0.1 lb/ac/annum, and similar figures were quoted by Jensen (1940), Jensen and Swaby (1940), Parker (1955) and Hannon (1956). Delwiche and Wijler

(1956) could only stimulate fixation by Azotobacter by the addition of very large amounts of sucrose. The addition of 10 tons/ac gave 40 lb/ac N, and 78 tons/ac gave 344 lb/ac N. Allison et al (1947) concluded that artificial inoculation of soils with Azotobacter cultures (the Russian "Azotogen") did not increase soil N. The tropical analogue of Azotobacter is the acid-tolerant Beijerinckia, which has also been reported at high altitudes in the Canterbury Alps (A.H. Nordmeyer; pers. comm.). It may be significant on leaf surfaces ("phyllosphere"), according to Ruinen (quoted by Norris, 1962; in Tropical Pastures Symposium). The ubiquitous and numerous Clostridium has been claimed to fix 20 to 50 kg/ha/annum, but these values are very extreme and unlikely.

Photosynthetic bacteria (Rhodospirillum rubrum) have been suggested as N-fixers, but their ecological niche is extremely restricted, and they cannot be widely significant. Some autotrophs (Aerobacter aerogenes, Nocardia spp., Desulphovibrio desulphuricans) are very common in soils, but probably fix only small amounts of N if combined-N is not available. From time to time some fungi (Phomopsis casuarinae, Pullularia spp.) and some yeasts (Saccharomyces spp., Rhodotorula spp.) have been suggested as N-fixers, but their contributions must be very small.

Perhaps 20 spp. of blue-green algae (Nostoc, Anabaena, Scytonema spp.) are known to fix N in some specialised habitats (Allison and Hoover, 1935), but their contribution does not seem to be large, except in paddy-fields. Tchan

and Beadle (1955) reported accessions of about 3 lb/ac/annum in arid soils of low pH, and the data of Cameron and Fuller (1960) confirmed this. Henzell and Norris (1962; in Tropical Pastures Symposium) reported an experiment by Allen under optimal simulated paddy conditions, where Anabaena cylindrica fixed 5760 lb/ac/annum. A figure of 70 lb/ac/annum might be more realistic.

## II. 2 (4) SYMBIOTIC NITROGEN FIXATION.

New Zealand agriculture is completely dependent on N fixation by legumes, principally White Clover. The literature dealing with the many aspects of this Rhizobium/legume symbiosis is voluminous, and will not be discussed here. Excellent reviews have been published by Hallsworth (1958), Allen and Allen (1958) and the CSIRO Committee of Tropical Pastures (1962), while Raggio and Raggio (1962) have reviewed literature pertaining to root nodulation, under many headings.

Unexplained increases of soil N over short periods of time (Allison, 1955) led Stevenson (1953, 1957, 1958, 1959) to conclude that many species of growing plants may utilise atmospheric N in some way, after considering the possible small accessions of N from sources other than nodulated legumes and non-legumes. After a series of N<sub>15</sub> experiments, on which some doubt has been cast (di Menna, 1962; pers.comm.) she concluded that many common members of several families (Rubiaceae, Myoporaceae, Myrtaceae, Verbenaceae, Araliaceae) have leaf-gland

symbiotic relationships with N-fixing bacteria or blue-green algae. Very large increases of soil N were reported and some rather sweeping conclusions drawn regarding the ecological significance of these leaf-gland symbioses. Her work should be verified or disproved as soon as possible. Norris (in Tropical Pastures Symposium) reported N-fixation by Anabaena azolla as a leaf-gland symbiont on the water-fern Azolla, and also on Gunnera macrophylla. Norris noted Orr's observation of bacterial leaf-gland symbiosis in yams, and possibly in some members of the Myrsinaceae.

An association of an Ascomycetous fungus with an alga is a lichen, and in about 8% of lichens blue-green algae (Nostoc, Rivularia) have been recorded. Azotobacter may be a third symbiont. Bond and Scott (1955) have reviewed N fixation by this symbiotic mechanism in lichens such as Leptogium and Collema, and in the liverwort Blasia pusilla. Scott (1956) verified this work, but gave no quantitative figures.

There have been reports of nodulation in many other genera, and a short discussion is useful. Unfortunately, N fixation is often not verified by definitive experiments, and quantitative figures are sadly lacking. Baylis (1961) reviewed nodulation in native New Zealand plants and reported their presence in some species of Agathis, Dacrydium, Phyllocladus and Podocarpus, as well as Discaria, Sophora and Coriaria. Mycorrhizae in Pernettya macrostigma and Griselinia littoralis (both widespread at Franz Josef) have been examined (Morrison,

1957; Baylis, 1959), but fixation does not seem to occur.

Purshia tridentata fixes atmospheric N, and Salix spp. have also been suggested (Palmer and Miller, 1961). Dryas Drummondii in Alaska has been shown to fix quite large amounts of N and influence the growth of cottonwoods (Schoenicke, 1957-58). Fixation by Calluna vulgaris and Pinus sylvestris has been suggested, but was disproved by Bond and Scott (1955). Norris reported (Tropical Pastures Symposium) fixation by at least 22 species of Ceratozamia (Cycadaceae) in Australia, which have symbiotic blue-green algae in root nodules. From this discussion it can be seen that the list of possible N-fixing plants is quite long, and in view of the demonstrable importance of N in soil and plant co-development, recognition of further N-fixing plants by careful experiments with isotopic N should be encouraged.

The significance of non-leguminous symbiotic N-fixation has only recently been appreciated, and it appears that some of these plants may become as important to forestry as legumes are to agriculture. There have been some excellent reviews of the topic, and only a few extra points will be mentioned here. A great deal of the work on non-leguminous N-fixing plants has been carried out by Bond and his co-workers at Glasgow, and at least eight of their papers have been partially reviewed by Bond (1958a, 1959). These are listed below (footnote), as they contain much important material not covered in the reviews.

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Ferguson and Bond (1953), Bond et al (1954), Bond (1955), Fletcher (1955), Bond (1956, 1957a, 1957b, 1958b).

Further work has been done by Harris and Morrison (1958), Morrison and Harris (1958) and Pearson and Rogers (1962). More practical applications of this ability to fix N were discussed by Lawrence and Hulbert (1950) and Lawrence (1951b). Classical microbiological work attempting to isolate the endophyte in non-leguminous nodules was reported by Quispel (1954, 1955, 1960). It is worthwhile listing the nodulated non-leguminous Angiosperms capable of fixing N: (After Allen and Allen, 1958; p.95).

Betulaceae	<u>Alnus</u>	17 spp.
Eleagnaceae	<u>Eleagnus</u>	10 spp.
	<u>Hippophae</u>	1 spp.
	<u>Shepherdia</u>	2 spp.
Myricaceae	<u>Myrica</u>	1 spp.
Rhamnaceae	<u>Ceanothus</u>	7 spp.
	<u>Discaria</u>	1 spp.
Casuarinaceae	<u>Casuarina</u>	12 spp.
Coriariaceae	<u>Coriaria</u>	1 spp.

There seems to be considerable doubt over the total number of species in these genera; 65 spp. (Allen and Allen, 1958), or 190 spp. (Bond, 1958a).

The extreme taxonomic antiquity of the group, and the widespread and discontinuous nature of genera and species, presages great significance in the past. Most species listed above actively colonise bare areas, and they may have been the main original sources of N in soils of the post-glacial era. Peat pollen studies have revealed widespread Alder forests during this period in Britain, and Alder is still very important

as a sub-pioneer on Alaskan recessional moraines. The same function is being carried out by Coriaria spp. at Franz Josef. Qualitative work on Coriaria has been done by Harris and Morrison (1958) and Bond (1958b), and the geography of the genus discussed by Good (1930). The effect of agriculture is to substitute legumes for these non-legumes. The artificial use of Alder, Coriaria and others in forestry may be restricted by the limited distribution of the endophyte, as inoculation is not possible at present. The endophytes have not yet been successfully isolated, and little is known about strain efficiency and cross-inoculation. Certain species may fix large amounts of N: Alnus glutinosa fixed 0.2 to 0.45 lb/annum per tree (Ferguson and Bond, 1953), and Alnus crispa 55 lb/ac/annum (Crocker and Major, 1955). One Myrica gale plant grown in N-free nutrient solution contained 3 gm. N after three years (Bond, 1955). Efficiency of fixation in vitro is high, as the following table taken from Ferguson and Bond (1953) shows:

Table 2.. Comparative Nitrogen fixation by Red Clover, Field Pea, Alder and Myrica.

	mg. N per gm. DM of nodule.	Nodule DM as % of whole plant DM.
<u>Red Clover</u>	703	4.0
<u>Field Pea</u>	539	5.3
<u>Alder</u>	814	2.2
<u>Myrica</u>	420	6.6

In short-term experiments small additions of combined-N have

increased total weight of nodules markedly in Alnus and Myrica, but the ratio of nodule weight to weight of plant, is decreased. With high levels of added N total weight of nodules also falls. Presumably this affects fixation of N.



## II. 3. PHYSICAL FEATURES OF THE FRANZ JOSEF REGION.

### II. 3 (1) GLACIAL PHYSIOGRAPHY.

It is not known who was the first European to see the Franz Josef Glacier, but von Haast was the first of many scientific observers. Explanations have been advanced by von Haast (1879), Harper (1893) and Willett (1950) for the existence of living glacier ice 700' above sea level, and it is thought that the combination of low-altitude snow-line, large glacial névé/trunk ratio, high precipitation and extremely steep descent is responsible. During the last century most glaciers in both Hemispheres have suffered severe ablation and/or terminal retreat (Matthes, 1945). The Franz Josef Glacier is no exception to this trend, the firn line having sunk approximately 200 feet, together with a terminal retreat of at least a mile in the last 60 years, and the loss of over 300 million cubic yards of ice from the lower mile of the glacier. Another 250 million cubic yards has been lost by ablation of the trunk (Harper, 1946). Several authorities (Harrington, 1951; Harper, 1934, 1935; and Brodrick, 1906) attempted to explain this phenomenal ice wastage. Suggate (1949) attempted to correlate movements of the terminal face with precipitation, hours of sunshine and temperature; but it is admitted by Speight (1940a+b) that no definite explanation can be advanced.

The Franz Josef Glacier flows roughly South to North in a valley between the Kaiser Fritz and Baird ranges in South

Westland at right angles to the strike of the country rocks, and its terminal face lies 14 miles from the sea at Lat. S  $43^{\circ}25'30''$  and Long. E  $170^{\circ}10'58''$ . The Glacier is 8.7 miles long with a mean width of 0.53 miles, the total fall being 8929' (Douglas and Harper, 1895). Odell (1960) estimated the mean grade as 1064'/mile. It is fed from the Geikie, Salisbury, Chamberlain and Davis snowfields which, together with several smaller fields, comprise a huge névé totalling 5882 acres (Bell, 1910). The South edge of the predominantly smooth névé abuts several high peaks and arêtes on the main Dividing Range of the Southern Alps, and is much broken by bergschrunds before descending 1500' in half a mile as the Grand Ice Fall. The surface of the Glacier is at all points exceedingly crevassed with many spectacular seracs. The catchment basin of the Franz Josef is estimated as 27.4 square miles (17,436 acres), of which 17.9 square miles is snow and ice; the névé/trunk ratio being approximately 5:1 (Douglas and Harper, 1895).

The melt water is highly charged with glacial flour, carries a large bed-load, and flows to the sea in the Waiho River, a typical flat shingle bed river with braided streams. The Waiho catchment includes several tributaries, the major ones being the Callery and Tatare, and the total area is 176 square miles (112,640) (von Haast, 1879). Many smaller tributaries flow into the valley of the Franz Josef Glacier as steep cataracts and waterfalls from small subsidiary hanging glaciers and glacial cirques, which often markedly contribute to erosion of the ice.

The valley of the Franz Josef has the U-shaped cross-section and level floor characteristic of glacially eroded terrain. Until recently the Franz Josef was engaged in active corrasion, and (unlike the Tasman Glacier) exhibited no signs of pulling away from the walls (Speight, 1940b). Prominent on the valley floor are a number of roches moutonnées, now partially afforested on their gentle Northern slopes. They exhibit glacial striae, have a smoothly mammilated and hummocky surface, and show typical crag-and-tail structure with the steep face towards the Glacier. The valley walls rise precipitously and have a prominent trim-line about 300' above the valley floor (representing the past position of the firn line), which approaches and meets the valley floor a little North of the suspension bridge over the river. A large terminal moraine, mostly covered by a rata-kamahi forest association, is seen 41 chains North of the roches moutonnées. The terminal face was stable at this point for a considerable time prior to the start of the latest retreat c. 1850 AD, and there are several contemporaneous lateral moraines on the valley sides. The frequent fluctuations of the terminal face have allowed the river to emerge from the ice at various points across the valley floor, and its meanderings while flooded and carrying high bed loads have laid out a system of low terraces. It is these terraces that have been sampled.

One of the outstanding characteristics of the Franz Josef Glacier is its extremely rapid rate of movement, due to its

steepness and high névé/trunk ratio. This has been noted by many observers, and measurements of this movement have varied greatly according to the season, distance from the terminal face and side walls, and method of observation. The results of many measurements were summarised into a table by Suggate (1949). Harper and Douglas (1894) reported speeds of 24 to 207"/day two miles from the face; Harper (1894) measured one mile up the glacier and reported 5 to 132"/day; while Bell (1910) recorded a speed of only 9 to 24"/day close to the terminal. Further, Suggate (1949, 1951) mentioned, whilst discussing the effects of climate on the Glacier, that the effects of a heavy or light snow season seem to become apparent five years later at the terminal face, which indicates a speed of about 200"/day. Both Suggate (1951) and Odell (1955) have reported on the progress of aeroplanes which crashed onto the Glacier: one travelled 2 miles between March 1950 and January 1955 at 70"/day; the other, 180 chains in 6 years 4 months at 60"/day. The surface ice flows faster than the lower ice, and horizontal shear planes are seen in the terminal face, showing marked overthrusting.

In "Glacial and Pleistocene Geology" Flint (1957) showed the Franz Josef Glacier reaching to the sea and extending far North and South of the Waiho River. The present retreat seems to be the latest of four since c. 1600 AD, each retreat being followed by successively smaller advances. The first serious attempt to chart accurately the position of the terminal face was made by Douglas and Harper (1895), when they mapped the face and

placed cairns on both valley walls to determine the extent of any future ablation. In 1910 Bell placed seven pegs at various points across the valley and these were used as base marks by several investigators, chiefly Speight (1914, 1921, 1934, 1940a). He observed that the visible terminal face is not necessarily the true end of the retreating glacier, as there may be buried stagnant ice in front of the terminal. Measurements made with the aid of Bell's pegs were summarised by Speight (1934). We have the following sources of information concerning terminal fluctuations (Harper, 1946):

1. An engraving of a photograph by Pringle (1867), from von Haast (1879).
2. Reports by Douglas and Harper (1895), Harper and Douglas (1894).
3. Four papers by Speight (1914, 1921, 1934, 1940a).
4. Bell's comprehensive geographical report (1910).
5. Photographs and paper by Harper (1926).

To which may be added:

6. A photograph in a paper by Suggate (1949).
7. Recent maps by Suggate (1951) and Odell (1960).
8. New Zealand Aerial Mapping Company photo. no. 1552/20 - Cook River to Kanieri Survey. (1948).
9. R.N.Z.A.F. aerial photographs (1 April 1953).
10. Frequent photographs by the New Zealand Geological Survey from 1950.

From all this it is possible to summarise the glacial fluctuations since c. 1850.

1. Very slow secular retreat from 1876 to 1910, with several minor advances during this time.
2. Rather faster retreat till 1921.
3. Advance till 1933 to approximately the position at 1910.
4. Rapid retreat of 1200 yards till 1946.
5. Rapid advance of about 400 yards till 1950.
6. Very rapid retreat of at least 1000 yards since 1950, with widespread ablation of the Glacier trunk.

A deep lake (about 40 by 20 chains) South of Wilson and Park Rocks was formed during the retreat from 1933 to 1946. Buchanan (1951) has reported that torrential rain (42.5") during February 1949 produced large floods and filled the lake with gravel, and it is now quite non-existent. This storm perhaps initiated the present large-scale retreat.

## II. 3 (2) GEOLOGY OF THE FRANZ JOSEF AREA.

Geological information was given by von Haast (1879) and Harper and Douglas (1894), but the latest work has been done by Wellman and Willett (1941) and Lillie et al (1954, 1957). The final authority is the map by the New Zealand Geological Survey (1958). Broad structural features of Westland were reviewed by Wellman (1956), and Gunn (1960) mapped the physical geology of the Franz Josef in some detail.

The South faces of Sentinel, Harper, Teichelmann and Park Rocks form a NW to SE straight line (striking  $140^{\circ}$ ) called the Park Fault, and the roches moutonnées are the remnants of the eroded relatively upthrown NE side of this fault. The stress of the Alpine Fault, which passes along the ends of the truncated spurs adjacent to the narrow coastal plain, has been further relieved by the formation of major E to W faults spaced 200 yards apart for at least 6 miles SE of the Alpine Fault. Examples of these faults are Duck creek, Hugh creek, Arch creek and Rope creek, and they typically have a highly brecciated zone

for 100 yards to the South, and are relatively upthrown to the North. Gunn also recognised two synclines and an anticline parallel to the Alpine Fault, which also passed through the valley of the Fox Glacier.

The Geological map of New Zealand (1958) shows four zones through which the Franz Josef flows. These are, from South to North along the Glacier:

- |   |   |
|---|---|
| "ghi" - greywacke                                   | Undifferentiated greywackes of Canterbury, Auckland and the North Island Main ranges. (Jurassic and Permian)                      |
| "9" - Chlorite zone schists)                        | } Otago, Alpine and Marlborough schists. (High stress and low temperature metamorphics of the Lower Mesozoic and Upper Paleozoic) |
| "8" - Biotite zone schist and gneiss.               |   |
| "7" - Garnet-Oligoclase zone gneiss.                |   |
| "q" - Alluvium, low terraces, moraine outwash, etc. | Recent - Haweran. (Holocene.)   |

The river gravels and boulders seem to be an homogenous mixture of these rock types over the areas sampled for this research.

## II. 3 (3) THE CLIMATE AT FRANZ JOSEF.

The following data (Table 3) are condensed from full climatological records at the town of Waiho (Franz Josef) during the period July 1953 to December 1960, and held at the New Zealand Meteorological Service, Wellington.\* The station is 392' ASL and at Lat.  $43^{\circ}23'$  S, Long.  $170^{\circ}11'$  E; about 3 miles from, and 300' below, the sampling sites. Concise figures are

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\* The assistance of T.R. Detwyler in collating these records is gratefully acknowledged.

not available, but the rainfall on the sites probably exceeds the recorded rainfall by at least 25"/annum. Mean temperature is slightly lower, and there are more frosts (P.J. King, pers. comm.).

The climate would probably be superhumid-microthermal (AC'r), according to Thornthwaite's climatic region classification. Garnier (1958) has discussed at length regional climates of Westland.

Table 3.. Climate at Franz Josef.

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year or Mean
<u>Mean Rainfall (Inches)</u>												
17.4	15.4	17.0	17.4	16.6	12.8	12.0	17.4	17.0	20.6	17.8	18.2	199.6
<u>Mean raindays.</u>												
15	13	15	15	15	14	14	15	17	20	19	18	190
<u>Mean Temperature. (°F)</u>												
59.0	59.6	58.0	53.9	49.5	45.2	44.2	46.2	48.7	51.2	53.5	57.3	52.2
<u>Mean daily Maximum Temperature. (°F)</u>												
68.1	67.9	66.1	62.1	57.4	52.9	52.9	54.5	57.2	59.3	61.3	66.0	60.2
<u>Mean Daily Minimum Temperature. (°F)</u>												
49.8	51.2	49.8	45.7	41.7	37.6	35.5	38.0	40.3	43.1	45.7	48.7	43.9
<u>Per-cent relative humidity.</u>												
83	87	88	91	90	90	86	86	85	83	83	84	86
<u>Days of Ground Frost.</u>												
0.3	0.1	0.1	2.3	8.4	16.8	20.2	16.1	13.2	6.6	2.1	0.5	86.7
<u>Days of Screen Frost.</u>												
-	-	-	0.1	1.7	3.7	6.1	3.1	0.4	0.4	-	-	15.5



## II. 3 (4) SOILS.

The New Zealand Soil Map (Taylor et al, 1948) regards the soils of the Franz Josef area as either Recent soils from Alluvium (20a), or Moderately and strongly Podzolised Yellow Brown Earths and Podzols (8), and related Hill soils. However, Taylor and Cox (1956), on a very generalised map, showed either Gley Podzols (with moderately weathered Yellow Brown Earths, recent and gley soils) (7); or podzolised steep-land soils, related to weakly and very weakly weathering Yellow Brown Earths (with mountain soils, bare rock and ice) (12). More specifically, Gibbs et al (1950) mapped at 4 miles/inch the soils of the Waiho Valley as an Ikamatua sandy loam (Mk), a young to immature podzolic soil on undulating, rolling and hilly land. However, the soils of the sampling sites on the level flood plain of the Waiho River more closely approximated to the Hokitika gravelly sandy loam, a rapidly draining shallow soil formed under totara forest. A typical profile from Kokatahi is:

4" brown gravelly sandy loam

on stony gravels containing some sand.

In the natural state there would have been a 2-4" layer of dark brown matted mor humus on the surface. An analysis of a soil near Waiho is:

Table 4..    Analytical figures for Hokitika gravelly sandy loam near Waiho.

Depth (in)	1% cit. sol. $P_2O_5$ (%)	N (%)	C/N	pH	BEC (me.%)	Total bases (me.%)	%BS	Exch.	
								CaO (me.%)	K <sub>2</sub> O (me.%)
0-5	0.080	0.10	18	5.9	3.5	1.4	40	1.4	0.4

This soil would probably be a weakly accumulative, weakly enleached lithic soil from bouldery schist (Taylor and Pohlen, 1962). Steepland and forested soils so common near Franz Josef are best described by Wright and Miller (1952).

## II. 4 SOME BOTANICAL AND ECOLOGICAL FEATURES OF DEGLACIATED AREAS.

### II. 4 (1) DEGLACIATED AREAS IN ALASKA.

Theoretical aspects of plant ecology have been discussed at length by Clements (1916) and Tansley (1954). Clements introduced the concept of the "prisere" - the succession of communities first colonising bare ground - and the prisere is our main concern whilst studying Chronosequences of soils and vegetation on recessional glacial moraines. Tansley (1929) and Monsi and Oshima (1955) have reviewed and evaluated concepts of the succession process; whilst a more specific entity of biotic community and environment - the Ecosystem - has been well discussed by Tansley (1935) and Sjors (1955). The Ecosystem may be defined as "the whole complex of organisms and factors of environment in an ecological unit of any rank, the cubic extent of which is arbitrary and determined by the method of study".

Glacial fluctuation in South-East Alaska and Southern South America has been studied, prior to soil and plant investigations, by several authors\*, but their speculations on the deglaciation process are not of interest here. The problems of 'dating' glacial moraines have been well reviewed by Heusser (1953) and Zeuner (1958), and more detailed information on dendrochronology given by Lawrence (1950). Jansen (1962) has recently cast some doubt on dating by tree rings after  $C_{14}$

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\* Cooper (1937); Field (1937, 1947); Lawrence (1951a); Lawrence and Elson (1953); Lawrence (1958a); Lawrence and Lawrence (1959a).

experiments on a Kauri log. An interesting series of papers concerning lava flows on Mt. St Helens (Washington) have showed how radiocarbon dating can help plant succession studies (Lawrence; 1941, 1954, 1959b).

All this preliminary data has aided phytosociological investigation on moraines. Much of the material pertaining to South-East Alaska has been reviewed by Lawrence (1953, 1958b), and is largely based on work by Lutz (1930), Cooper (1923a+b+c, 1924, 1925, 1931, 1939) and Lawrence (1951b). Cooke and Lawrence (1959) contributed further material, and Zach (1950) discussed the probable climax vegetation of the region. The following generalised prisere has been recognised, but there are a number of xerarch and hydrarch variations:

<u>Stage</u>	<u>Possible age</u>	
Pioneer	0-10 years	Lichens, Mosses (eg. <u>Rhacomitrium canescens</u> ), <u>Epilobium latifolium</u> , <u>Equisetum variegatum</u> , then merging to <u>Dryas Drummondii</u> .
Sub-pioneer	10-60+	<u>Shepherdia canadensis</u> , <u>Alnus</u> ( <u>sinuata</u> , <u>tenuifolia</u> and others), in some cases <u>Lupinus nootkanensis</u> . <u>Salix</u> spp., usually a succession of prostrate to erect species.
Transition	60-100+	Invasion of sitka spruce ( <u>Picea sitchensis</u> ) and cottonwoods ( <u>Populus trichocarpa</u> and <u>P. tacamahaca</u> ) into Alder forest. <u>Alnus</u> 6-8" in diameter, and not regenerating.
Spruce/Hemlock	150-200+	Spruce may grow to 110' tall and 3' diam., but is gradually replaced by two species of Hemlock ( <u>Tsuga mertensiana</u> and <u>T. heterophylla</u> .)

<u>Stage</u>	<u>Possible age</u>	
Sub-Climax	10,000+ (?)	Association of hemlocks, cedar ( <u>Thuja plicata</u> ) and <u>Chamaecyparis nootkanensis</u> gives way to Muskeg association ( <u>Sphagnum</u> and <u>Carex</u> spp.)
Climax	(?)	Muskeg association, lodgepole pine ( <u>Pinus contorta</u> ) on the drier hilly areas. "Pit-pond" development may occur if the skink cabbage ( <u>Lysichitum americanum</u> ) establishes.

Ludi (1945) and Onthank (1951) reported some European variations on this succession. Palmer and Miller (1961) investigated a belt transect through the prisere near the Rotmoos Gletscher in Austria, where the pioneer was Saxifraga aizoides with lithophyte mosses, and the sub-pioneer various Salix spp.. The pioneer success of Saxifraga was attributed to the possession of an active perennial root system. Legumes and other proven N-fixers were not seen, which probably explains the slowness of the succession.

Some conclusions may be drawn from the above evidence:

1. The pioneers are generally not known N-fixers; their areal and floristic distribution being dependent on the number, proximity and mobility of their disseminules, and the rate of exposure and characteristics of bare moraine. Their source of N is not certain, but it is probable that meagre supplies of N from glacial flour, meltwater, rain, fungal, algal and yeast growth are sufficient to sustain plants with very low demands for N. They may have leaf-gland bacterial symbioses, or N-fixing 'phyllosphere' micro-organisms.

2. Dryas, Alnus, Purshia tridentata, Shepherdia, Ceanothus, Hippophae (and others), and some legumes, are sub-pioneers. Their presence and vigour is essential to the accumulation of OM, which is the most important effect of plant growth on the PM during the early stages of the prisere. Only lately have botanists started to realise this very important fact.

3. After a variable period of time other species dominate the N-fixing plants and eliminate them. This is the result of regenerative inability due to competition for light and nutrients, as previously explained.

4. The dominant species (usually conifers in the prevailing periglacial conditions) utilise the N accumulated earlier in the succession, which then continues for a variable but lengthy period. The prisere may be terminated by the slow adaption and alteration of floristic composition to meet changing conditions of soil and climate. Other "lines of succession" may be followed.

5. The inevitable soil degradation (leaching, podzolisation) changes the sub-climax/climax equilibrium, and "inferior" species of lower nutrient requirement may dominate if disseminules are available. Under suitable climates, bog species (in muskeg, pakihī) generally climax the succession. Renewed soil development is conditional on catastrophic landscape alteration, due to factors such as glaciation, earthquakes and severe erosion.

## II. 4 (2) THE FORESTS OF WESTLAND.

This topic is far too large to be adequately covered in this short Review, but a few standard references can be noted. Fleming (1962)(p.88) has dealt in a general manner with the onset of the Westland Piedmont Glacier during the last Glaciation (Otiran Stage), when the permanent snow-line was at least 3,500' lower than at present (Willett, 1950). Vegetation was completely eliminated during this Piedmont Glaciation, but tundra conditions (with tussock) prevailed on the coastal high terraces during the Interglacial before the subsequent valley glaciation. There may have been a small advance of beech from the North during the Interglacial, retarded by natural ecological barriers such as river valleys. The beech was probably later extinguished by the valley glaciers. Rata and kaikawaka colonised and survived on the hills, and remnants may still be found. Quite recently, podocarp-broadleaf forest (first manuka, then totara, kahikatea, together with broadleaf understory spp.) established on the high terraces, and later were invaded by rimu, miro and some other broadleaved species. Throughout this period podzolisation and the formation of pakihi bogs (with manuka and silver pine) was proceeding (Chavasse, 1962). Published detailed floristic lists for Westland's forest ecotypes are lacking, although Cockayne (1927; p. 86-89) devoted some space to a description of some communities. Later, Cockayne (1928) was able to treat this topic more satisfactorily, and described the communities of podocarps (p. 163-166); rata, kamahi and kahikatea (p.168-175); Westland sub-tropical rain forest (p.269) and the

Westland Botanical district as he knew it (p.394). The colonisation of river beds is described (p.209), and Appendix I contains a detailed floristic list of active colonising species.

More detailed and accurate descriptions of Westland forests have recently been compiled (Holloway, 1954a; Masters et al, 1955). From these, and the bulletin by Chavasse, the forests may be broadly grouped as follows:

1. Mountain protection forests East of the Alpine Fault; dominant rata-kamahi with Hall's totara and kaikawaka near the timber-line (3,500'), below the tussock and sub-alpine scrub. Rimu-miro-broadleaved forests are present at low altitudes, and these are generally even-aged old trees with little or no regeneration taking place. Some silver and mountain beech is seen in the North and South.

2. Hill forests West of the Alpine Fault; mainly of rimu-miro-broadleaves, being replaced by podocarp-beech or beech in the North and South. In basins between the hills pole rimu may sometimes be found.

3. The dense rimu terrace forests (with some miro and kahikatea, and an understory of broadleaved spp.) are very susceptible to the effects of PM and topography. Variations in slope, PM, degree of podzolisation and freedom of drainage provoke changes in forest structure. On flat ground, pakihis (with silver pine and manuka) and swamps (kahikatea) may be developed.

4. The recent flood plains, if still forested, support two main types of community: totara-matai on well-drained gravels, and kahikatea on wetter areas.



These communities occur in a complex mosaic, but some relationships between soils, landforms and forest types have been discerned. The climatic change hypothesis of Holloway (1954b, 1959, 1962), over which there has recently been some contention (Cumberland, in McCaskill, 1962), was partly formulated from the evidence of the Westland forests and their changing patterns. As the climate became cooler and drier the pakihi bogs have steadily been forested by a peripheral invasion of manuka, silver pine and lastly rimu. Another successional change conditional on the recent cooler and drier climate is the marginal advance Northwards and Southwards of the beech, as in the Taramakau valley. On the other hand, soil deterioration may preclude the advance of the beech, and the process may act in reverse. The climatic change has therefore forced the rimu from the mountains and onto the terraces, where it is replacing the silver pine and kahikatea of the erstwhile swamps.

#### II. 4 (3) BOTANY OF THE FRANZ JOSEF REGION.

Published references to the flora of the Franz Josef region are sadly lacking. Cockayne (1928)(p.170) gave a short list of some principal forest species present on the valley walls, which is reproduced in Appendix II; and Appendix I gives a broad picture of the river-bed priseral succession common in Westland. Cockayne also published (in Bell, 1910) a list of plants under 1470' altitude from the Franz Josef Glacier to the coastline (based on a list by Hamilton, 1879; unpublished), which contains 56 families, 148 genera and 287 species. Unfortunately, this

list is not arranged ecologically (according to seral communities), and therefore is not very useful. Consequently, botanical data reported in the following chapter has been compiled by field inspection with little help from the Literature.

The Flora of the Mount Cook National Park region has been described by Wall (1925) and Connor (1959). Wall discussed (p.34-36) moraine successions, and Connor's brief references to this ecological situation are based on this short account.

Although not strictly comparable with the Franz Josef successions they are of interest, as many of the same species are present. The pioneers include Epilobium melanocaulon, E. microphyllum, Poa Lindsayi, Muehlenbeckia axillaris, Raoulia australis, Poa novae-zealandia and others. Sub-pioneers such as Carmichaelia grandiflora, C. robusta, Poa Colensoi, Coprosma acerosa, Danthonia semi-annularis var setifolia and Dracophyllum longifolium are present. The direction of priseral succession is then diverted according to the habitat; either lateral moraine, steep shingle fans, morainic mounds or river flats. Scrub successions usually form on lateral moraines and fans, with mountain totara, celery pine, Olearia moscheta, Aristotelia fruticosa, Coprosma spp., Hebe spp., and Coriaria thymifolia. Where the moraine material is less bouldery grass communities are found, including Poa Colensoi, Deschampsia novae-zealandia and Poa caespitosa. River flats support tussock communities and Discaria toumatou. On the morainic mound at the junction of the Hooker and Mueller Glaciers; Discaria, Coriaria thymifolia and C. sarmentosa, Danthonia setifolia and scrub species occur discontinuously.

## PLATE 2.



Portion of the official vertical aerial photograph of the Waiho Valley, showing sampling Stages I to VI, and also "IX" and "X". (Taken on 13th April, 1948; from 11,000' altitude.)

## III. 1. RECOGNITION AND DESCRIPTION OF SUCCESSION STAGES.

## III. 1 (1) THE PRISERE.

The prisere at Franz Josef has been recognised and described by T.R. Detwyler\*, to whom this author is greatly indebted for much botanical and ecological information. The first part of the prisere has been divided into six Stages (denoted by Roman numerals) for this investigation, each of which will be described below. Plate 2 should be consulted for exact locations. Plant densities by species for individual communities have been determined by the point-centred quarter method (Cottham and Curtis, 1956) and the number of plants per hectare of any species is shown in the following floristic lists. The number of rooting stems per square metre may be derived by dividing by  $10^4$ . Following the description of the Stages and their communities short discussions will be made on the probable succession in the area and the place of Coriaria at Franz Josef.

STAGE I.. Situated 100 m. due SE of the carpark, and  $1\frac{1}{2}$  m. above stream. Surface quite devoid of macro-organisms.

STAGE II.. About 250 m. due E of waterfall on W side of valley, 200 m. S of kettle-hole near Park Rock. Approximately 8 m. above river bed. Terrace gently sloping ( $3^{\circ}$ ).

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\*Fulbright Scholar at Otago University during 1961.

<u>Stratum</u>	0 - 0.25 m.	Raoulia tenuicaulis	101,000
		Epilobium glabellum	45,000
		Poa novae-zealandiae	38,000
		Epilobium pedunculare	17,000
		(Parahebe linifolia	
		+Carmichaelia grandiflora	
		+others.)	4,000

Total 205,000

The red alga Trentepohlia is very common on all rocks, and there are many clumps of green Racomitrium moss. Other species occasionally seen are Gunnera albocarpa and Aristotelia serrata. The vegetation is distributed extremely discontinuously and large areas are virtually unaltered from Stage I.

STAGE III.. Flat river bed between Teichelmann and Strauchan Rocks; 1 m. above gently flowing stream.

<u>Stratum</u>	0 - 0.25 m.	Raoulia tenuicaulis	210,000
		Epilobium pedunculare	196,000
		Olearia avicenniaefolia	125,000
		Epilobium glabellum	89,000
		Poa novae-zealandiae	30,000
		Carmichaelia grandiflora	26,000
		(Danthonia cunninghamii	
		+ Holcus lanatus	
		+ Dactylis glomerata	
		+ Hebe salicifolia	
		+ Helichrysum bellidiodes	
		+ others	44,000
		Estimated moss cover = 20%	

Total 738,000

There is one small patch of the prostrate Carmichaelia nigrans var tenuis, and isolated individuals of Arundo conspicua and Gaultheria rupestris.

	0.25 - 2 m.	Carmichaelia grandiflora	12,000
		Danthonia cunninghamii	1,400
		Olearia avicenniaefolia	1,300
		Poa novae-zealandiae	500
		(Holcus lanatus	
		+ Dactylis glomerata	
		+ Coriaria arborea	
		+ several grasses)	1,400

Total 16,000

STAGE IV.. High and level terrace S. of Wilson Rock.

About 4 m. above old river bed.

<u>Stratum</u>	0 - 0.25 m.	<i>Pterostylis australis</i>	54,000
		<i>Carmichaelia grandiflora</i>	49,000
		<i>Angelica montana</i>	23,000
		<i>Pernettya macrostigma</i>	19,000
		<i>Lycopodium fastigiatum</i>	11,000
		( <i>Coprosma rugosa</i>	
		+ <i>Olearia avicenniaefolia</i>	
		+ <i>Haloragis</i> spp.	
		+ <i>Cyathodes fraseri</i>	
		+ <i>Poa novae-zealandia</i>	
		+ <i>Parahebe lyallii</i>	
		+ <i>Hypochaeris</i> spp.	
		+ <i>Helichrysum filicaule</i>	
		+ about a dozen others)	77,000
		<u>Total</u>	<u>235,000</u>
	0.25 - 2 m.	<i>Carmichaelia grandiflora</i>	27,000
		<i>Danthonia cunninghamii</i>	17,000
		<i>Coprosma rugosa</i>	12,000
		<i>Angelica montana</i>	10,000
		<i>Olearia avicenniaefolia</i>	6,000
		<i>Coriaria sarmentosa</i>	5,000
		( <i>Holcus lanatus</i>	
		+ <i>Olearia arborescens</i>	
		+ <i>Lycopodium fastigiatum</i>	
		+ <i>Gaultheria rupestris/perplexa</i>	
		+ <i>Anthoxanthum</i> spp.	
		+ <i>Hebe subalpina</i>	
		+ <i>Hebe salicifolia</i> )	13,000
		<u>Total</u>	<u>91,000</u>
	2 - 8 m.	<i>Coprosma rugosa</i>	2,200
		<i>Carmichaelia grandiflora</i>	800
		<i>Olearia avicenniaefolia</i>	1,500
		( <i>Hebe salicifolia</i>	
		+ <i>Dracophyllum longifolium</i>	
		+ <i>Gaultheria rupestris/perplexa</i>	
		+ <i>Olearia arborescens</i> )	300
		<u>Total</u>	<u>4,800</u>

STAGE V.. Lowest terrace NW of Strauchan Rock, only 1 m.  
above the level of Stage III.

<u>Stratum</u> 0 - 0.25 m.	Haloragis spp.	30,000
	Griselinia littoralis	19,000
	Coprosma lucida	17,000
	Mazus pumilio	15,000
	Coprosma rugosa	12,000
	Phymatodes diversifolium	6,000
	(Carmichaelia grandiflora	
	+ Corybas spp.	
	+ Pterostylis australis	
	+ Lagenophora pumila	
	+ Olearia avicenniaefolia	
	+ Hoheria spp.	
	+ Neopanax colensoi	
	+ Asplenium flaccidum	
	+ Angelica montana)	30,000

Total 129,000

There is also some Blechnum capense and Polystichum vestitum.

0.25 - 2 m.	Coprosma rugosa	17,000	
	Olearia avicenniaefolia	3,000	(20% dead or dying.)
	Coprosma lucida	2,300	
	Carmichaelia grandiflora	1,600	
	Phymatodes diversifolium	1,600	
	Danthonia cunninghamii	1,600	
	(Olearia arborescens		
	+ Griselinia littoralis		
	+ Neopanax colensoi		
	+ Angelica montana		
	+ Coriaria plumosa		
	+ Hebe subalpina)	5,200	

Total 33,000

2 - 8 m.	Olearia avicenniaefolia	15,000
	Coprosma rugosa	6,000
	Carmichaelia grandiflora	5,000
	Hebe subalpina	2,000
	Olearia arborescens less than	1,000

Total 29,000

STAGE VI.. Terrace 3 m. above and due E of Stage V, due N of Strauchan Rock.

<u>Stratum</u> 0 - 0.25 m.	<i>Mazus pumilio</i>	16,000
	<i>Phymatodes diversifolium</i>	10,000
	<i>Corybas</i> spp.	8,000
	<i>Griselinia littoralis</i>	7,000
	<i>Coprosma lucida</i>	6,000
	<i>Haloragis</i> spp.	4,000
	( <i>Coprosma rugosa</i>	
	+ <i>Neopanax colensoi</i>	
	+ <i>Carmichaelia grandiflora</i>	
	+ <i>Hebe subalpina</i>	
	+ <i>Coprosma</i> spp.	
	+ <i>Pterostylis australia</i>	
	+ <i>Nertera dichondraefolia</i>	
	+ <i>Lagenphora</i> spp.	
	+ <i>Grammitis heterophylla</i>	
	+ several others)	12,000
	<u>Total</u>	<u>63,000</u>

0.25 - 2 m.	<i>Phymatodes diversifolium</i>	18,000
	<i>Griselinia littoralis</i>	4,000
	<i>Coprosma rugosa</i>	4,000
	<i>Coprosma lucida</i>	4,000
	<i>Polystichum vestitum</i>	4,000
	( <i>Neopanax colensoi</i>	
	+ <i>Schefflera digitata</i>	
	+ <i>Olearia arborescens</i>	
	+ <i>Pterostylis australis</i>	
	+ <i>Myrsine divaricata</i>	
	+ <i>Olearia avicenniaefolia</i>	
	+ <i>Asplenium flaccidum</i> )	6,000
	<u>Total</u>	<u>40,000</u>

2 - 8 m.	<i>Olearia avicenniaefolia</i>	14,800(2% dying)
	<i>Coprosma rugosa</i>	3,000(3% dying)
	<i>Carmichaelia grandiflora</i>	3,000(3% dying)
	( <i>Gaultheria rupestris</i> /	
	<i>perplexa</i>	
	+ <i>Coriaria arborea</i> )	600(All dying)
	<u>Total</u>	<u>21,400</u>

A number of general trends may be noted from these floristic lists:

1. The Pioneers of Stage II are not known N-fixing plants,



with the exception of the isolated and small individuals of Carmichaelia. As in Alaska, their distribution is patchy and is the result of co-incidental habitat and disseminule factors, as previously explained. The red alga covers the rocks but probably has no effect on soil formation, whereas the moss and Raoulia may collect particles of wind-blown silt.

2. The Sub-pioneers of Stage III include the vigorous, bushy legume Carmichaelia, which grows here to a height of 1 m. . Eventual dominants (Olearia avicenniaefolia) make their first appearance, very closely associated with individuals of Carmichaelia. Their vigour seems directly proportional to their radial distance from the root system of the Carmichaelia, showing their dependence on the N being added to the Ecosystem by this plant. The community presents a more homogenous appearance, though there are still large clearings between groups of plants.

3. The vegetation of Stage IV grows uniformly to a height of approximately 2 m., where Coprosma and Olearia are becoming dominant. Carmichaelia, though still dominant in the middle stratum, is suppressed and is not regenerating.

4. This process is accentuated through Stages V and VI, with eventual upper stratum dominance of Olearia, which is also not regenerating. Young broadleaf (Griselinia littoralis) is becoming common. Carmichaelia is being eliminated from the prisere, and there are no other (undisputed) N-fixers taking its place. Thus, after only a very short time the bush is about 7 m. high, rather dense, and many mosses, ferns and lycopods are present. The situation is utterly unlike that obtaining in Stages I, II and III.

### III. 1 (2) FURTHER SUCCESSIONAL COMMUNITIES ON OLDER SURFACES.

Explorations of the area from Stage VI to the terminal moraine in the company of other botanists\* have elucidated the probable continuation of the succession in this region. Stages "VII" to "X" have been tentatively recognised as a prelude to further investigations. The main vegetational trends appear to be:

1. The diversification of species, with an increasing number of Coprosma and Olearia spp.

2. The intermediate dominance of broadleaf (Griselinia littoralis) and fuschia (Fuschia excorticata).

3. The eventual development of a tiered forest structure with Southern rata (Metrosideros umbellata) and kamahi (Weinmannia racemosa) as upper-tier dominants; a lower tier of Olearia spp, Griselinia, Carpodetus serratus, Schefflera digitata, Myrsine divaricata etc.; and a well-developed shrub layer over the flora of the forest floor. Occasional sapling Hall's totara (Podocarpus hallii) and miro (Podocarpus ferrugineus) are seen.

4. There is a deep humus layer on top of the mineral soil, with local wet areas. The dark undershrub conditions are suitable for the seedling development of rimu (Dacrydium cupressinum). This Stage, tentatively shown as X on plate 2, is probably sub-climaxed by rising podocarp dominance, with rimu, miro and Hall's totara in the canopy over 30 m. . Rata and kamahi would be relegated to a sub-canopy at 20 m. .

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A preliminary investigation of (the proposed) Stage IX, again by the point-centred quarter method, yielded the following list of species:

<u>Stratum</u>	0 - 0.25 m.	<i>Nertera dichondraefolia</i>	60,000
		<i>Phymatodes diversifolium</i>	30,000
		<i>Astelia nervosa</i>	10,000
		<i>Neopanax colensoi</i>	5,000
		<i>Clematis paniculata</i>	5,000
		(plus several others)	5,000

Total 110,000

0.25 - 2 m.	<i>Blechnum capense</i>	16,000
	<i>Astelia nervosa</i>	16,000
	( <i>Polystichum vestitum</i>	
	+ <i>Coprosma ciliata</i>	
	+ <i>Coprosma propinqua</i>	
	+ <i>Melicytus ramiflorus</i>	
	+ <i>Phymatodes diversifolium</i>	
	+ <i>Neopanax colensoi</i> )	14,000

Total 46,000

2 - 8 m.	<i>Olearia avicenniaefolia</i>	600
	<i>Coprosma propinqua</i>	400
	<i>Schefflera digitata</i>	400
	<i>Coprosma lucida</i>	400
	<i>Coprosma ciliata</i>	400
	<i>Myrsine divaricata</i>	400
	( <i>Weinmannia racemosa</i>	
	+ <i>Fuschia excorticata</i>	
	+ <i>Carpodetus serratus</i>	
	+ <i>Neopanax colensoi</i>	
	+ <i>Blechnum capense</i>	
	+ <i>Coprosma colensoi</i>	
	+ <i>Metrosideros umbellata</i> )	1,400

Total 4,000

Above 8 m.	<i>Metrosideros umbellata</i>	900
	<i>Olearia avicenniaefolia</i>	400(all dying)
	<i>Olearia ilicifolia</i>	100(all dying)
	<i>Carpodetus serratus</i>	100

Total 1,500

Some additional rough "grab" soil samples were taken from Stage "X" and two other older soils (under rimu-rata-kamahi) in

the district during December, 1962; when the analysis of samples from Stages I to VI had been completed. The results are of interest as they are indicative of possible nutrient levels for older soils of the sequence, and will be discussed in a later section.

### III. 1 (3) THE PLACE OF CORIARIA AT FRANZ JOSEF.

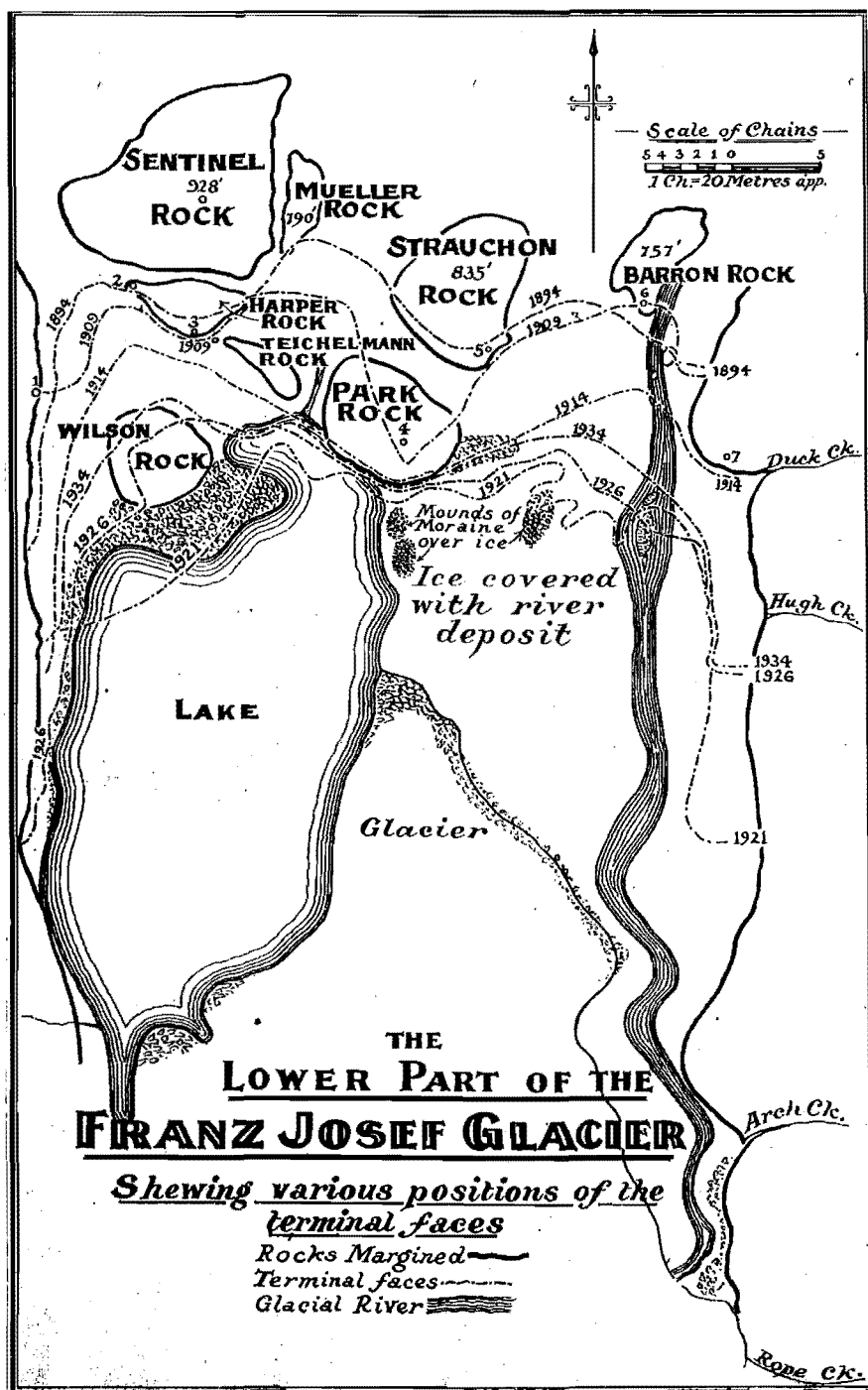
One of the most spectacular botanical features of the Franz Josef region is the extensive growth and vigour of tutu (Coriaria genus) on scree slopes of the valley walls, and as a riparian community on the river flats. Due to extensive interspecific hybridisation the taxonomics of the genus are indeterminate, but at least four species of Coriaria have been identified at Franz Josef - arborea, sarmentosa, lurida and angustissima (plumosa?). Unfortunately it was not possible to sample Ecosystems including Coriaria, as the plants are generally found rooted in water-washed silt between large talus boulders on steep slopes. The number, variety and vigour of other species existing within the Coriaria thicket (which may reach considerable heights) bear witness to the N-fixing efficiency of the plant in such a harsh habitat. All plants examined were heavily nodulated and their foliage was deep green and luxurious. The length of their branch internodes showed extremely rapid growth; many stems elongating more than 60 cm. per annum. One attempt was made to sample the Ecosystem around an individual Coriaria 30 cm. tall growing about 20 cm. above a stream 5 m. due W of Strauchan Rock. The situation is not strictly comparable to the other pits sampled

under Carmichaelia, for at least three reasons:

1. Running water may be adding nutrients to the Ecosystem.
2. There was much very fine micaceous silt around the plant, trapped by the Raoulia mat covering the boulders.
3. It is extremely difficult to determine accurately the age of the surface and the plant itself.

However, as it is impossible to sample Coriaria on the steep valley walls, and as the plant requires constant supplies of water and will not grow under conditions of physiological drought on the well-drained terraces, a compromise was reached and the pit-site chosen with as much care as possible. Great care should be exercised when interpreting the results presented for this pit sample, and they are to be regarded as only indicative of the possible importance of Coriaria at Franz Josef. Like Carmichaelia, Coriaria is eliminated from the successional communities of the valley walls at an early stage, although its arboreal habit allows longer persistence than Carmichaelia. In view of the present widespread distribution of Coriaria throughout New Zealand where bare ground is exposed and the water and nutrient regimes are satisfactory, it is very probable that this plant was the major source of N in the soils of the post-glacial era in New Zealand. If this is so its importance in soil development in priseral successions cannot be under-estimated. This viewpoint is strongly contested by Baylis (pers. comm.).

## PLATE 3.



Terminal positions during retreat of the Glacier. (Reproduced from a figure in a paper by Speight, 1940a.)

### III. 2 THE AGES OF SURFACES.

An accurate assessment of rates of change of soil properties is impossible without positive knowledge of the surface ages. The retreat of the Glacier has been fairly accurately charted over the years, making it relatively easy to assign a maximum age to any given point on the river bed; but unfortunately the river bed is made of terraces laid down by the meandering Waiho River which are not necessarily related to the position of the terminal face. Estimations of surface ages may thus become more in the nature of informed guesses.

STAGE I.. The area sampled lay close to a running stream and was frequently covered by floods. An age of zero can be confidently assigned to this surface.

STAGE II.. The area was covered with water or ice in 1940 and Suggate (1951) shows it covered with ice in 1951. Thus the maximum age is only 11 years. Photographs taken by the New Zealand Geological Survey show that the terrace was not present on 9th January 1954, but was definitely present on 30th August 1956. Intermediate photographs are unfortunately not available. Therefore, Stage II was not older than 7 years at the time of sampling, and probably nearer 6 years.

STAGE III.. The actual sampling sites in Stage III, mostly due W. of Strauchan Rock, have not been covered with ice for at least 70 years, but the Waiho flowed between Teichelmann and Park Rocks for a long time. When the lake near Park Rock emptied in 1949 (Buchanan, 1951) floods catastrophically altered

this surface, destroying any previous vegetation. This is confirmed by Mr. Peter McCormack of Franz Josef (pers. comm.). The maximum age is therefore only 13 years. The R.N.Z.A.F. aerial photograph of 1st April 1953 shows the river covering a small portion of the surface, but it was diverted shortly afterwards. An age of 12 years will be assumed.

STAGE IV.. This level terrace S of Wilson Rock has a scarp about 4 m. above the valley floor. Wilson Rock was first seen in 1894-95 (Harper and Douglas, 1894), but the rock was an elusive one and disappeared before 1910, to be exposed again in 1921 (Speight, 1921). Evidently vegetation established on the rock from this time. However, Speight reported in 1934 that "...the Glacier is pushing moraine over Wilson Rock, destroying plants growing there since 1921. Only a small portion of the Rock, in the NW corner, is now visible.". Soon after this, rapid and permanent retreat took place, and the terrace was smoothed by water as the ice was removed. A maximum age of rather less than 30 years is indicated. The present terrace is a remnant of a surface laid down c. 1935, much of which has been removed by the water produced by the great retreat till 1946. Therefore, the age of the surface is 25 years.

STAGES V AND VI.. Stage V occupies a small crescent-shaped terrace 3 m. lower than, and to the W of, Stage VI, and is only 1 m. above Stage III. The whole area was definitely covered by ice in 1867 (from a plate in von Haast's book), but was exposed in 1894, according to Harper and Douglas. However, no sign of



the terraces can be seen in their photographs, and water is still actively flowing around Strauchan Rock at this time. Bell has included with his report some photographs, presumably taken near 1909, and one of these shows very clearly the two terraces now carrying Stages V and VI. Thus, they were not present in 1894 (68 years ago), but were present in 1909 (53 years ago). A maximum age of 60 years is suggested. It is thought that the Stage VI surface will not have been altered by floods between Mueller and Strauchan Rocks, but Stage V could easily have been so affected, and would appear to be a little younger than Stage VI. The vegetation on Stage V has a mean height of 5 m., and that of Stage VI 6-7 m. . Dr.P. Wardle (pers. comm.) suggests that a maximum growth rate of Olearia avicenniaefolia in that climate would be 6" (15 cm.) per annum. Stage IV carries Olearia 2 m. high. Applying these figures as a rough check gives an age difference from IV to V of 20 years, and from IV to VI of 26 to 33 years. If Stage IV is 25 years old; Stage V is 45 years old, and Stage VI 51 to 58 years. The absence of further conclusive and accurate data based on observation of the terraces precludes better estimations. Thus, Stage V will be regarded as 45 years old, and Stage VI 55 years.

Summary: The following ages in years are postulated for the respective surfaces:

Stage I	... Nil
Stage II	... 6
Stage III	... 12
Stage IV	... 25
Stage V	... 45
Stage VI	... 55

### III. 3 SAMPLING PROCEDURE.

#### III. 3 (1) CHOICE OF SAMPLING SITE.

Three pits were dug within each Stage, represented by an even-aged surface with a homogenous plant community. The pit-sites were not randomly chosen; Selection was entirely subjective and was guided by two basic principles:

1. that an effort should be made to sample only areas with an "intermediate" composition of boulders and fine materials (Plate 4a). Excessively stony or silty areas were avoided. However, in the older Stages the thick humic material made visual pre-determination of the surface lithology very difficult. In addition, the presence of one or more large boulders beneath the surface and within the sampling volume could greatly alter the volume occupied by fine materials. The large variations in weight of air-dry "fines" less than 2 mm. in the pits are indicative of the sampling difficulties encountered. Nevertheless, some uniformity was achieved, despite the problems presented by the mechanically heterogenous PM.

2. that maximum variability of vegetal material between pits within any Stage be attempted, considering always the need for uniformity of PM. It was thought desirable to obtain samples from pits with a wide range of variability of plant cover, allowing an assessment of maximum and minimum growth and nutrient accumulation rates. The range of weights of plant material tabulated in Appendix III is indicative of the inherent natural variability of a plant community homogenous to a botanist or

forester dealing only with numbers of plant individuals.

### III. 3 (2) SAMPLING PROCEDURE.

Having chosen the exact site for any pit, a flat square wooden frame with internal dimensions of exactly 1 m. by 1 m. was assembled around the bush or tree. The living vegetation was first removed with a heavy knife, slasher or saw, and packaged in clearly labelled hessian sacks or paper bags. The surface layer of litter (the L layer) was included in this category, and also any living roots extracted from the mineral soil or humic material on the forest floor. Secondly, all the surface humic material (the F/H layer) was carefully removed with a sharp knife and packaged separately in heavy paper bags. In most cases this layer was clearly separated with a sharp boundary from the underlying mineral soil. Next, the mineral soil was removed with a spade and trowel and sieved through a  $\frac{1}{4}$ " square-hole garden sieve onto a large hemstitched duck canvas sheet with brass eyelets in each corner. Any roots remaining on the sieve were included with the living plant material, first removed, and any stones greater than  $\frac{1}{4}$ " discarded after thorough shaking. Boulders in the pit were prised loose with a small crowbar and discarded after carefully cleaning any adhering fine material off their surfaces with a paintbrush. When a sufficient pile of gravel had accumulated on the canvas it was weighed at field moisture with milk scales (graduated to 60 lb) hung from an adjacent branch or an upright pole wedged at 45° from the ground with boulders. After thorough mixing,

the fine material was spread thinly over the canvas, marked in a grid pattern, and a sub-sample of 5% or 10% of the weight taken systematically with a large sugar scoop and stored in a covered gallon billy, and the remainder of the fines discarded. In this manner the pit was excavated with a level floor to the bottom of the upper humus-enriched horizon, taking care to separate the brown upper horizon from the lower conspicuously grey PM. The various subsamples from any horizon were spread on another canvas, thoroughly mixed by hand and an approximately 10 lb. aliquot taken, carefully weighed and packaged. The depth of the upper layer was measured from the F/H-soil interface, and the lower horizon excavated to a total depth of 33 cm. from the interface. No material, vegetal or mineral, was removed from outside the arbitrary boundaries of this one-third cubic metre soil Ecosystem, and all living stems and foliage growing within the confines of the metre-square frame were included. An attempt was made to compensate for the volumes of boulders projecting into the pit from the sides or bottom.

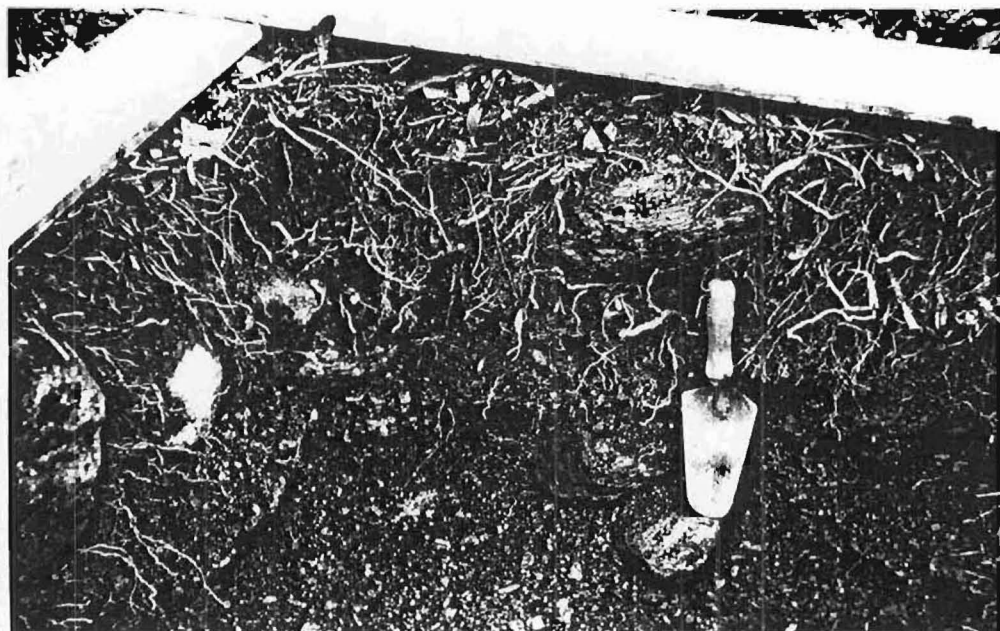
This lengthy procedure was considered satisfactory, but it has a number of faults, which will be discussed in a later section.

Thus, the Ecosystem was divided, sampled and analysed in four distinct portions, some of which are not present in the younger Stages. These portions are:

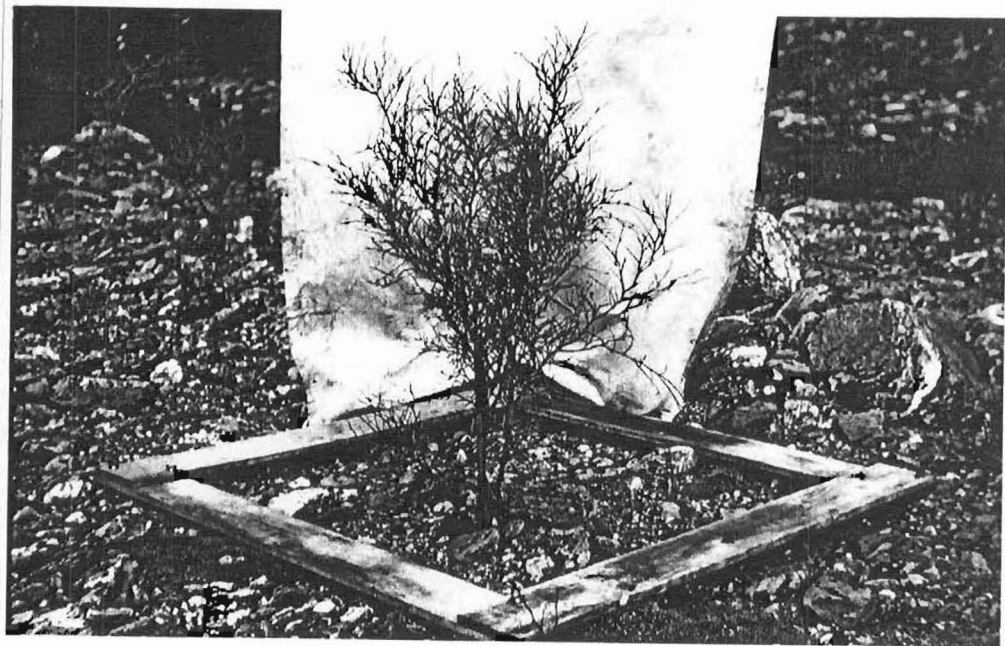
1. The living tree or bush, Raoulia mat, mosses, ferns and other ground species, together with the thin L layer of recently deposited leaves and twigs. All living roots in the mineral and F/H layers were included. (Designated V)



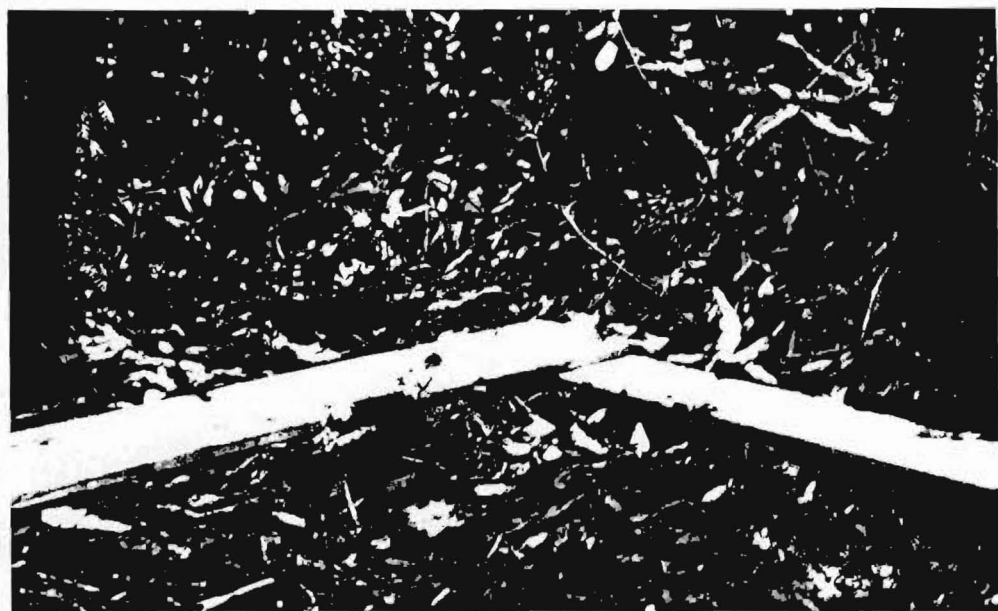
(a) An "intermediate" proportion of boulders and finer gravel on Stage I.



(b) Profile of completed pit, Stage VI.  
(Depth = 33 cm.)



(a) Carmichaelia grandiflora on Stage III., showing metre-square in position for pit excavation. (Plant is  $\frac{1}{2}$  m. tall.)



(b) General view of sampling site on Stage VI. Litter removed and upper surface of F/H revealed.

2. The F/H layer; a dark, greasy, compacted mor humus, profusely interwoven with roots. (Designated F/H)

3. The brown humus-enriched upper horizon of the mineral soil, generally less than 10 cm. deep. (Designated Upper horizon)

4. The underlying grey PM, with only occasional roots, down to a depth of 33 cm. . (Designated Lower horizon)

The first three Stages had soils with no differentiation into upper and lower horizons and no F/H; Stage I had no vegetation (V). Pits from Stages IV, V and VI were divided into four Ecosystem portions, as outlined above.

### III. 4 ANALYTICAL METHODS.

#### III. 4 (1) SAMPLE PREPARATION.

Upper and Lower horizon mineral matter. The various 10 lb. aliquots were thoroughly air-dried and sieved through a 2 mm. square-hole sieve. The fractions were weighed, and a portion of the sub-2 mm. fraction finely ground in a Wiley mill for chemical analysis. The weight in the pit of air-dry (AD) fine material (sub-2 mm.) in grams per square metre to the depth of the horizon (or to 33 cm. in Stages I, II and III.) was calculated from the formula:

$$\text{AD sub-2 mm.fines (g/m}^2\text{/horizon)} = \frac{\text{lb.sub-}\frac{1}{4}\text{" fines in pit at field moisture} \times \text{gm. AD sub-2 mm. fines from aliquot}}{\text{lb. moist aliquot weighed in field.}}$$

A factor of 8.92 converts g/m<sup>2</sup>/horizon to lb./ac/horizon.

F/H material. This was broken up by hand into shallow metal trays, dried for a short time at c.  $70^{\circ}\text{C}$  in an oven, and weighed. A one-tenth subsample was taken by careful quartering, and dried to constant weight. This was ground first in a coarse mill, and a portion further ground in a Wiley mill with No.8 sieve plate.

V material. Leafy portions were weighed green and a one-tenth sub-sample taken if the quantities were unmanageable. This was dried to constant weight and ground coarsely. Tree trunks and heavy branches were weighed green, broken up with heavy secateurs and a circular saw into small disks not exceeding  $\frac{1}{2}$ " thickness, and a sub-sample equal to one-tenth of the green weight dried to constant weight. This was eventually ground once, incorporated with the coarsely-ground leaves and twigs, and a representative portion of the whole ground finely for analysis.

The finely ground samples from the Wiley mill were stored in 2 oz. screwtop glass jars. The extra grab-samples taken from the older soils were simply air-dried and the material less than 2 mm. finely ground.

### III. 4 (2) ANALYTICAL PROCEDURE.

Standard analytical procedures and methods were used throughout this research.

1. Oven-dry weights: at  $105^{\circ}\text{C}$ .
2. Loss-on-ignition: on F/H only; at  $500^{\circ}\text{C}$ .
3. Reaction: Determined on mineral matter and F/H according to the procedure outlined by Metson (1956); using a 1:2.5 ratio



of distilled water (1:5 for F/H) shaken for an hour, left overnight and four readings taken with a Radiometer pH meter equipped with glass-calomel electrode.

4. Organic Carbon: The modified Schollenberger-Allison dichromate method described by Metson (1956) was used.

Appropriate corrections were made for high-carbon materials.

5. Nitrogen: A semi-micro Kjeldahl method using Selenium catalyst was employed for all samples. (Metson, 1956).

6. Organic Phosphorus: The ignition method as described by Walker and Adams (1958) was used. Colour readings were made at 700 u on a Coleman spectrophotometer. Phosphorus in V and F/H was determined by the method of Kitson and Mellon (1944), using a molybdovanadophosphoric acid colour development measured at 470 u on a Coleman spectrophotometer. Some total P measurements were made by the  $\text{HF-HNO}_3$  digestion described by Metson (1956), and finally determined by the colorimetric molybdovanadophosphoric acid method.

The following results are all calculated on an oven-dry basis, and in most cases have been considerably "rounded-off".

Percentage Loss on Ignition (LOI%) was calculated by the formula of Metson (1956):

$$\text{LOI}\% = 100 - (\text{Ash}\% \times \text{Moisture Factor})$$

The linear regressions of  $y$  (nutrient) on  $x$  (time base of graph) are expressed as the formula

$$y = a + bx$$

In the following sections,  $P_t$  means total P extracted by N.  $\text{H}_2\text{SO}_4$  after ignition,  $P_a$  is inorganic P extracted by N.  $\text{H}_2\text{SO}_4$  without ignition, and  $P_o$  is organic P calculated by difference. "Total" P is the P determined by the  $\text{HF-HNO}_3$  method, and in these soils should closely approximate the  $P_t$ .

Table 5..

Detailed Volume-Weights of Ecosystem Separates.

Stage	Pit	Mineral Material (less than 2 mm.)					F/H			V	
		Upper Horizon		Lower Horizon		Mean of Upper plus Lower of 3 pits	Weight (g/m <sup>2</sup> )	Mean of 3 pits	LOI%	Weight (g/m <sup>2</sup> )	Mean of 3 pits
		Depth (cm)	Weight (g/m <sup>2</sup> )	Depth (cm)	Weight (g/m <sup>2</sup> )						
I	1	33	55,700	-	-	66,600	-	-	-	-	-
	2	33	77,900	-	-		-	-	-	-	-
	3	33	66,300	-	-		-	-	-	-	-
II	1	33	132,900	-	-	91,300	-	-	-	170	220
	2	33	73,700	-	-		-	-	-	370	
	3	33	67,200	-	-		-	-	-	130	
III	1	33	110,000	-	-	90,700	-	-	-	590	1600
	2	33	74,900	-	-		-	-	-	1220	
	3	33	87,200	-	-		-	-	-	2980	
IV	1	8	24,400	25	49,000	119,100	6380	4490	29.5	5960	5610
	2	6	40,500	27	89,400		3420		22.3	3900	
	3	9	36,700	24	117,200		3660		22.1	6970	
V	1	5	16,400	28	68,300	83,900	1670	2020	52.5	3910	3520
	2	15	40,400	18	35,300		2090		49.4	3190	
	3	14	41,700	19	49,600		2300		55.0	3470	
VI	1	9	48,100	24	86,800	87,800	2920	3620	55.4	4490	8440
	2	8	12,600	25	58,800		2980		63.0	8310	
	3	10	11,400	23	45,800		4970		52.2	12,530	

Table 5a..The weight of Organic Matter in F/H.(All figures in g/m<sup>2</sup>)

<u>Stage</u>	<u>Pit</u>	<u>Weight OM</u> (Wt. <u>F/H</u> X LOI%)	<u>Weight OM</u> (Carbon X 1.72)
IV	1	1880	1570
	2	760	680
	3	810	740
V	1	880	760
	2	1030	970
	3	1270	1140
VI	1	1620	1500
	2	1880	1610
	3	2590	2210

Mean Values for each Stage.(Calculated from the wt. F/H X LOI%)

IV.....	1150
V.....	1060
VI.....	2030

### Mean Weights of V and F/H

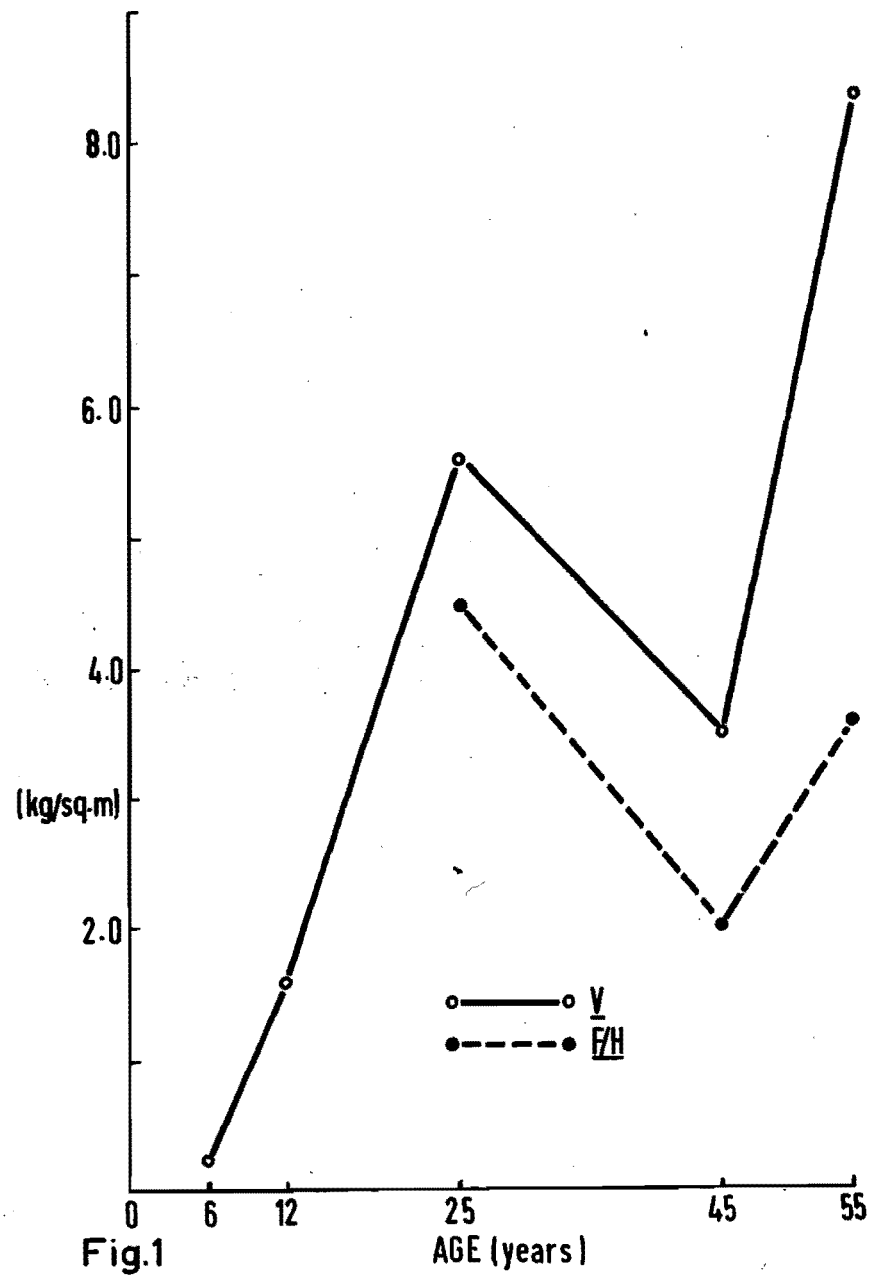


Fig.1

IV? See Table of Contents  
 III. 1. VOLUME-WEIGHTS.

See Table 5 and Figure 1.

1. There are large variations in volume-weights of upper and lower horizons, probably unavoidable considering the nature of the material sampled.

2. The large variations in volume-weight of mineral material between pits of any Stage are the basic reason for many of the observed variations in amount of any nutrient (see following tables) between the pits.

3. A very prominent feature of the V and F/H weights is the large accumulation in Stage IV, with a decrease in Stage V. This higher value in Stage IV might only be an apparent effect due to the method of sampling and the inadvertent choice of particular areas for sampling. However, it could be a real effect: Stage IV may represent a period of intense vegetal proliferation with corresponding heavy return of litter to the surface of the ground.

4. From approximately 20 years to 55 years there has been an increase of F/H from nil to over  $3600 \text{ g/m}^2$ , with a maximum of  $4970 \text{ g/m}^2$ ; about  $100 \text{ g/m}^2/\text{annum}$ . However, the accumulation to the level found in Stage IV occurs very much faster than this. Assuming accumulation is negligible till 15 years, 10 years' accumulation equals  $4500 \text{ g/m}^2$ , about  $450 \text{ g/m}^2$ . In pit 1 of Stage IV this rate of accumulation is greatly exceeded.

See Table 5a.. Weight of OM in F/H.

1. Theoretically, the weight of C ( $\text{g/m}^2$ ) times 1.72 should equal the amount of OM present. This can also be computed by multiplying the weight of F/H ( $\text{g/m}^2$ ) by the percentage Loss on Ignition.

2. Quite reasonable agreement has been reached between figures computed by these two methods in Table 5a., considering that the factor 1.72 is not really applicable to forest soils, and that "bound" water may contribute to LOI.

3. The mean values of OM for each Stage show a better progression from IV to VI than do the dry matter weights of above-surface litter residues. The reduction of the previous disproportionate influence of Stage IV is due to the low LOI values for the pits of this Stage.

4. The low LOI values in this Stage are due to the activity of worms, which have mixed mineral matter from the upper horizon with the F/H. Worms were not present in the F/H of Stages V and VI, because the surfaces on which these Stages are found are isolated from the valley walls by river beds. Worms cannot cross Stage III and colonise Stages V and VI.

### III. 2 REACTION OF MINERAL SOIL AND F/H.

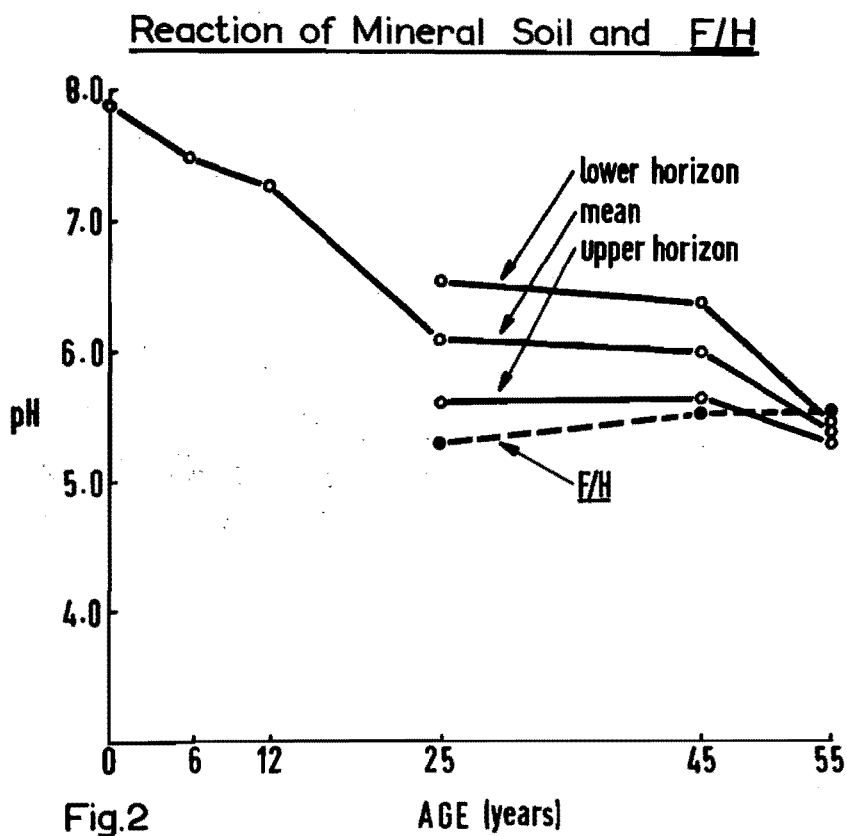
See Table 6 and Figure 2. Detailed figures are in Appendix III (a).

1. There is a rapid decrease in the upper horizon over 55 years from 7.89 to 5.29. The lowest value recorded (4.96) was in Stage VI, pit 1.

Table 6..Reaction of mineral soil and F/H.

	<u>Upper</u>	<u>Lower</u>	<u>Mean of both horizons</u>	<u>F/H</u>
<u>Stage</u>				
I	7.89	-	7.89	-
II	7.50	-	7.50	-
III	7.26	-	7.26	-
IV	5.61	6.55	6.08	5.30
V	5.63	6.37	6.00	5.51
VI	5.29	5.45	5.37	5.54





2. There is a quite rapid decrease of pH in the first three Stages.
3. Note the marked effect of afforestation on pH, especially of the upper horizon, between Stage III and Stage IV.
4. The lower horizon is less changed than the upper until after Stage V.
5. Note the almost unchanged pH of both horizons from Stage IV to Stage V.
6. The rapid drop from Stage V to Stage VI could perhaps be correlated with the elimination of Carmichaelia and other plant species changes.
7. Note the tendency for pH of both upper and lower horizons in Stage VI towards the same level.
8. pH of the F/H has not changed much from Stage IV to Stage VI.

### III. 3      ORGANIC CARBON.

See Table 7. and Figure 3. Detailed figures are in Appendix III (b).

1. The regressions have very satisfactory correlation coefficients:

$$\text{Ecosystem:} \quad y = -113 + 96.8x \quad (r = 0.939)$$

$$\text{Upper+Lower+F/H:} \quad y = -97 + 41.8x \quad (r = 0.980)$$

$$\text{Upper+Lower:} \quad y = -24 + 23.6x \quad (r = 0.987)$$

2. There is a very rapid accumulation of C in the Ecosystem at  $96.8 \text{ g/m}^2/\text{annum}$ , according to the regression.

Table 7..

Organic Carbon.

(Mean values of 3 pits per Stage.)

(All figures in g/m<sup>2</sup>)

Stage	Upper Horizon	Lower Horizon	F/H	<u>V</u>	Upper + Lower	Upper + Lower + <u>F/H</u>	Ecosystem
I	92	-	-	-	92	92	92
II	96	-	-	35	96	96	131
III	129	-	-	567	129	129	696
IV	338	209	579	2225	547	1126	3351
V	814	285	554	1426	1099	1653	3079
VI	728	534	1031	3497	1262	2293	5790

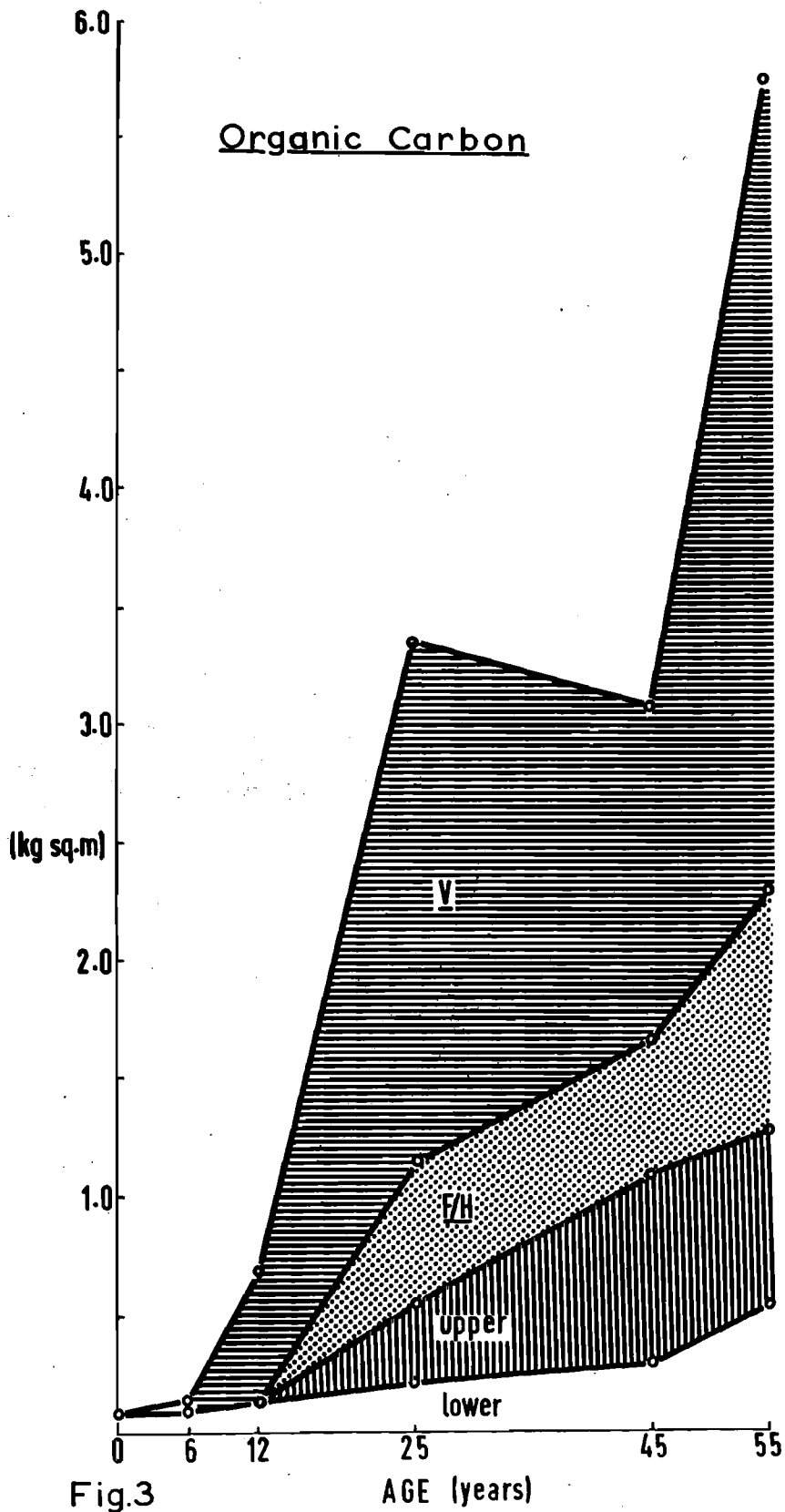


Fig.3

3. There are virtually unchanged levels in the lower horizon, except after Stage V.

4. Note the pronounced effect of the large contribution of V and F/H in Stage IV. Carbon in the mineral soil increases steadily.

5. The low weights of V and F/H in Stage V are to some extent compensated for by relatively higher %C, with respect to Stage IV.

6. No apparent "steady-state" has yet been reached.

7. There is a fairly high level of C in Stage I; this must be due either to experimental error or to the presence of algal tissue invisible to the eye. There is a slight possibility of OM being deposited by the nearby running stream.

8. The very high quantity of C being held in the V is of interest. This proportion (over 50%) would probably be lower in older soils.

9. The effect of the organic cycle is prominent; C is added to the F/H and thence to the upper horizon. The effect is hardly seen in the lower horizon.

### III. 4. NITROGEN.

See Table 8. and Figure 4. Detailed figures are in Appendix III (c).

1. The regressions have extremely satisfactory correlation coefficients.

Ecosystem:	$y = 9.1 + 3.02x$	( $r = 0.961$ )
Upper+Lower+ <u>F/H</u> :	$y = 1.9 + 2.36x$	( $r = 0.985$ )
Upper+Lower:	$y = 5.1 + 1.48x$	( $r = 0.992$ )

Table 8..Nitrogen.

(Mean values of 3 pits per Stage.)

(All figures in g/m<sup>2</sup>)

Stage	Upper Horizon	Lower Horizon	<u>F/H</u>	<u>V</u>	Upper + Lower	Upper + Lower + <u>F/H</u>	Ecosystem
I	8.7	-	-	-	8.7	8.7	8.7
II	12.5	-	-	0.6	12.5	12.5	13.1
III	16.8	-	-	20.9	16.8	16.8	37.7
IV	22.9	22.6	28.3	48.4	45.5	73.8	122.2
V	55.3	19.7	30.6	28.8	75.0	105.6	134.4
VI	47.1	36.4	47.6	38.3	83.5	131.1	169.4

# Nitrogen

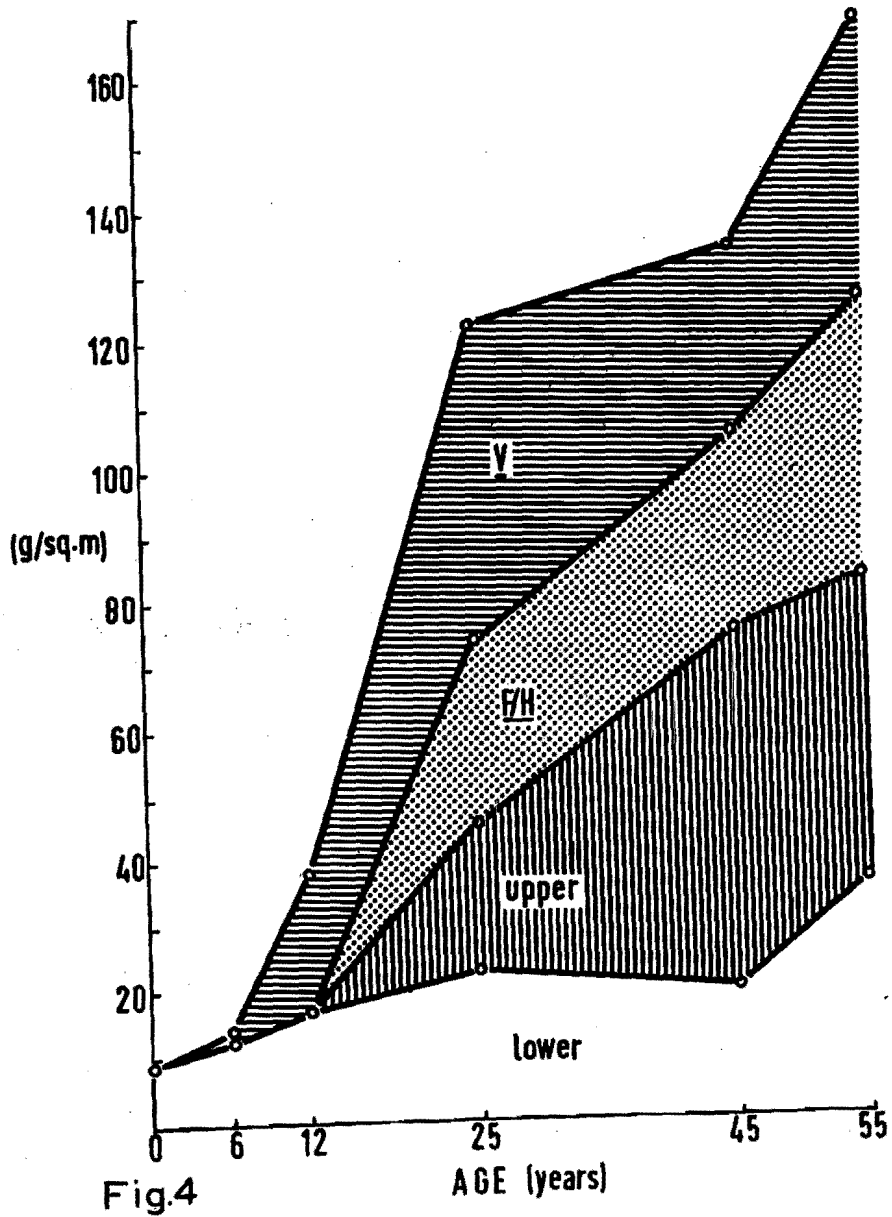


Fig.4

2. There is a close similarity to the graph of organic C accumulation, although there is no drop in Stage V.

3. No apparent "steady-state" has yet been reached.

4. There is quite a high level of N in Stage I; due to the possible presence of N-fixing algae and other micro-organisms, some N in the PM, and the possible addition of N from the nearby running stream.\*

5. The high proportions of N held in the V of Stage III later fall - compare with graph of organic C. (Figure 3.) There is a rapid rate of accumulation in Upper+Lower+F/H ( $2.36 \text{ g/m}^2/\text{annum}$ ).

6. The amount of N in the lower horizons remains virtually unchanged until Stage V, showing that the organic cycle (and possibly leaching) are only beginning to affect this horizon after half a century.

7. The highest level of N attained ( $189 \text{ g/m}^2$  in Stage VI pit 3) indicates the efficiency of Carmichaelia as an N-fixer. By difference from the lowest level ( $7.2 \text{ g/m}^2$  in Stage I pit 1) there is an extreme increase of  $181.8 \text{ g/m}^2$  in 55 years, or  $3.3 \text{ g/m}^2/\text{annum}$ . However, the rate of increase from Stage II to Stage IV exceeds this. Carmichaelia is the dominant plant in the communities of these Stages. From lowest ( $10.0 \text{ g/m}^2$  in Stage II pit 3) to highest level ( $142.3 \text{ g/m}^2$  in Stage IV pit 1) the annual increment is nearly  $7 \text{ g/m}^2/\text{annum}$ ; about 62 lb/ac/annum.

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\* A sample of water from the Waiho River near Stage I was analysed by Mr. H. Horn (Chemical Services Department, Lincoln College), and there was less than 0.5 p.p.m of  $\text{NO}_3\text{-N}$ .



Table 9..      Total and inorganic Phosphorus.      (Upper and Lower horizons and F/H.)

(Mean values of 3 pits per Stage.)

(All values expressed as parts per million.)

Stage	Upper Horizon		Lower Horizon		Mean of Upper and Lower		F/H	
	P <sub>t</sub>	P <sub>a</sub>	P <sub>t</sub>	P <sub>a</sub>	P <sub>t</sub>	P <sub>a</sub>	P <sub>t</sub>	P <sub>a</sub>
I	747	731	-	-	747	731	-	-
II	725	682	-	-	725	682	-	-
III	745	712	-	-	745	712	-	-
IV	709	640	774	733	742	687	805	518
V	701	613	752	721	727	667	1177	548
VI	643	517	727	709	685	613	1080	430

Table 9a.."Total" Phosphorus.

(All results in parts per million.)

Stage	Pit	Portion	P <sub>t</sub> .(by H <sub>2</sub> SO <sub>4</sub> )	"Total" P. (HF-HNO <sub>3</sub> )
I	1	(soil)	744	1065
VI	1	( <u>F/H</u> )	1108	935
VI	1	(Upper)	610	648

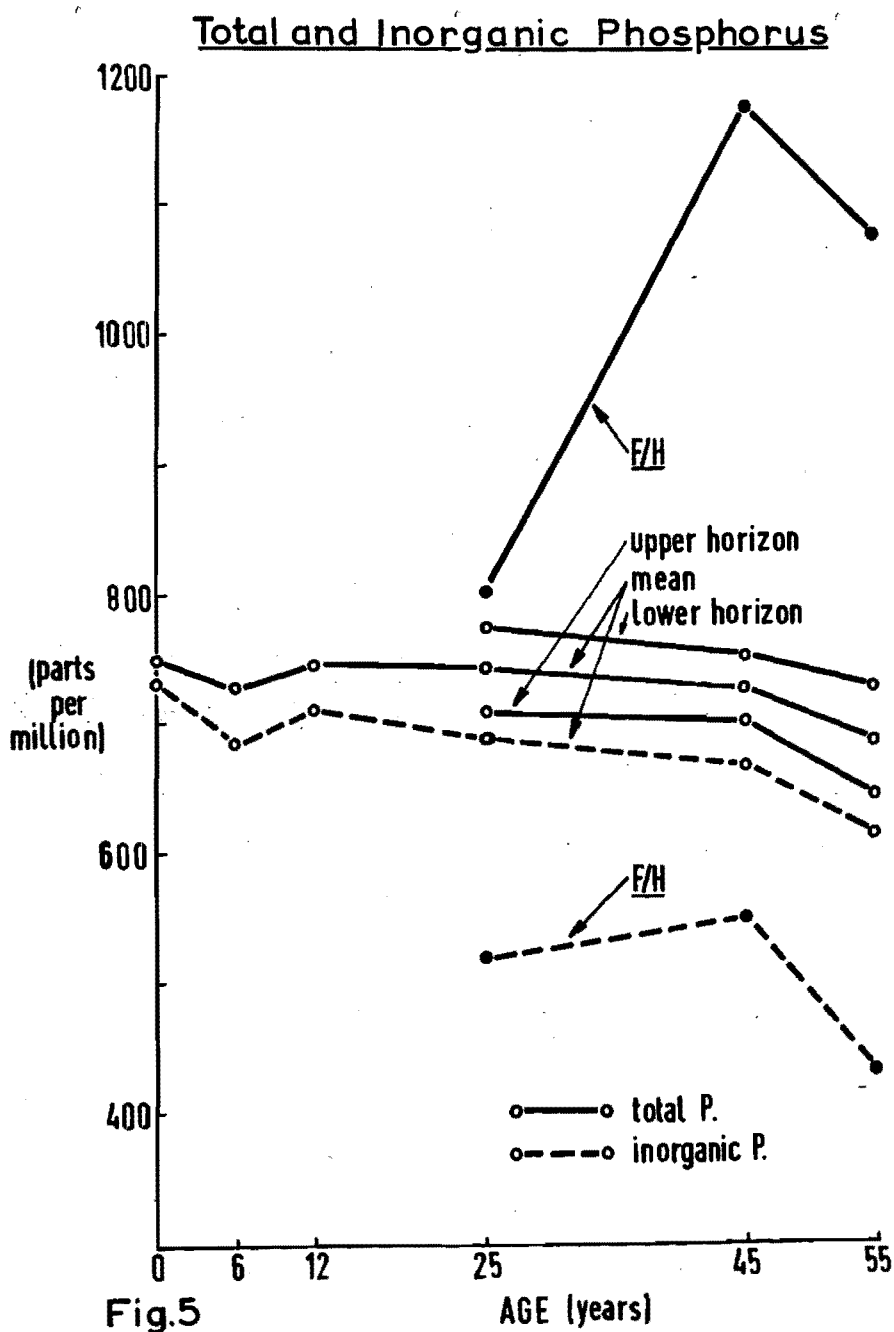


Table 10..      Total and inorganic Phosphorus.      (Upper and Lower horizons and F/H)

(Mean values of 3 pits per Stage)

(All values expressed as  $\text{g/m}^2$ )

Stage	Upper Horizon		Lower Horizon		<u>F/H</u>		Upper + Lower + F/H	
	P <sub>t</sub>	P <sub>a</sub>	P <sub>t</sub>	P <sub>a</sub>	P <sub>t</sub>	P <sub>a</sub>	P <sub>t</sub>	P <sub>a</sub>
I	49.75	48.68	-	-	-	-	49.75	48.68
II	65.29	61.60	-	-	-	-	65.29	61.60
III	67.54	64.39	-	-	-	-	67.54	64.39
IV	24.07	21.60	65.11	61.50	3.70	2.44	92.88	85.54
V	23.45	20.51	38.22	36.40	2.37	1.11	64.04	58.02
VI	15.06	12.09	46.15	44.99	3.89	1.55	65.10	58.63

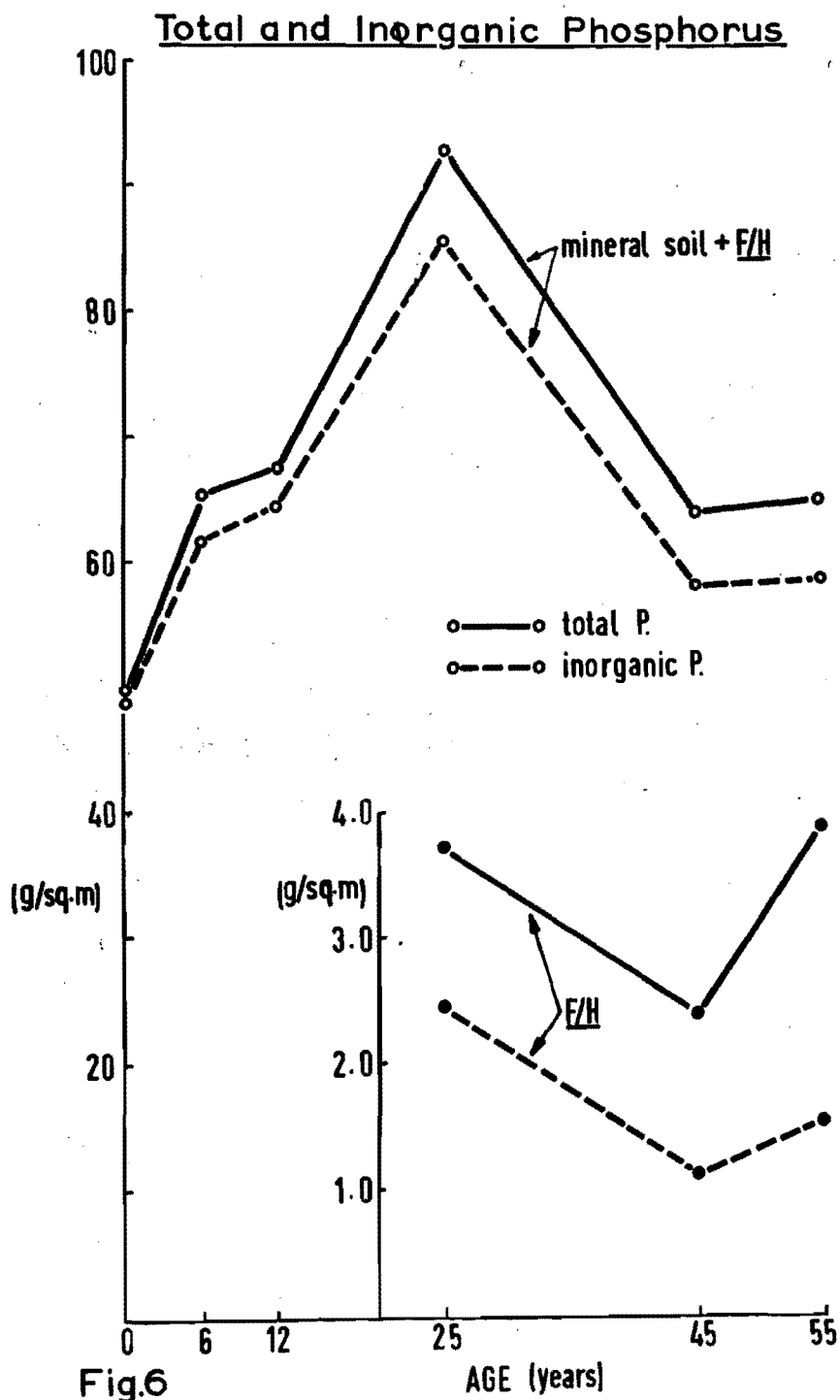


Fig.6

### III. 5 TOTAL AND INORGANIC PHOSPHORUS.

(1) Parts per million.

See Table 9 and Figure 5. Detailed figures are in Appendix III (d).

1. This table and graph show trends in P levels better than the following graphs, as they are uncomplicated by the widely variable weights of mineral matter, V and F/H.

2. The trend of  $P_t$  is fairly clear and consistent. The regression of the mean figures is:  $y = 748 - 0.80x$  ( $r = 0.757$ ). Some trends may be noted:

- (a) The mean values decrease after Stage IV; the ultimate level is lower than in Stage I.
- (b) The higher levels of  $P_t$  in the lower horizon (compared with the upper) trend downwards, probably due to increasing removal by roots after Stage V.
- (c) Phosphorus has been removed from the upper horizon by the vegetation and re-deposited in the F/H, which shows high levels of  $P_t$ . However, the trend of  $P_t$  in the upper horizon is downwards.
- (d) The high levels of  $P_t$  in the F/H, which increase with time, clearly show the effect of the organic cycle. The high concentrations of  $P_t$  in the F/H of Stages V and VI compensate for their lower weights compared with Stage IV.

3. The trend of  $P_a$  levels in the mineral horizons is also consistently downwards, at a greater rate than  $P_t$ : the regression is  $y = 721 - 1.63x$  ( $r = 0.884$ ). Apart from Stage II the curve is very even.

4. No clear inference may be made from the present data about leaching of P from upper to lower horizons. It is perhaps possible that the high level of  $P_t$  in the lower horizon of Stage IV (774 p.p.m., compared with a PM value of 747 p.p.m. in Stage I) may be due to leaching, especially as there has not been much transfer of P to the F/H at this Stage. However, as all inorganic material larger than  $\frac{1}{4}$ ", in which differences of  $P_t$  and  $P_a$  may have a profound effect, was discarded at the pit, predictions about any leaching loss are not possible.

5. It is probable that the great majority of P in the PM is apatite (Calcium-bound), and (depending on particle size) this will be very readily available to plants. Some preliminary analyses on a small selection of the soils by Mr. J.D.H. Williams (Lincoln College) have confirmed this. However, the proportion of the  $P_t$  that is Ca-bound falls rapidly from virtually 100% in Stage I to less than 50% in the upper horizons of Stage VI.

6. See Table 9a.. "Total" Phosphorus

Stage I, (soil). "Total" P is very high compared to  $P_t$ ; the extracts contained numerous fine crystals resembling silica, which greatly increased the Optical Density. Apparently HF is not able to digest all the silica in unweathered schist. The crystals were not present in the other extracts. The method should be modified for unweathered PM samples; either a long pre-treatment with cold HF, or two hot treatments.

Stage VI, (F/H). No explanation can be advanced for the low "Total" P. Walker and Adams (1959) reported that several of their high-OM soils had lower "Total" P than  $P_t$ .

This was attributed to experimental error.

Stage VI, (Upper horizon). Some discrepancy is evident. However, if an allowable range of  $\pm 2\%$  experimental error due to the limitations of the method is applied  $P_t = 598 - 622$  and "Total"  $P = 635 - 661$ .

(2) Grams per square metre.

See Table 10. and Figure 6. Detailed figures are in Appendix III (e).

1. The regressions are:

$$\text{Total P: } y = 64.9 + 0.107x \quad (r = 0.170)$$

$$\text{Inorganic P: } y = 61.5 + 0.054x \quad (r = 0.098)$$

The correlation coefficients are poor, largely due to the disproportionate influence of Stage IV. A curvilinear regression might fit the values better.

2. The general increase in  $P_o$  is clearly seen; from about 2% to 10% in Stage VI. Specific figures are given in the following section.

3. The amount of  $P_t$  in the F/H is surprisingly constant, while  $P_a$  decreases markedly. Despite the large amount of F/H in Stage IV the amount of  $P_t$  is not proportionately large compared to Stages V and VI, as they have higher concentrations of  $P_t$ .



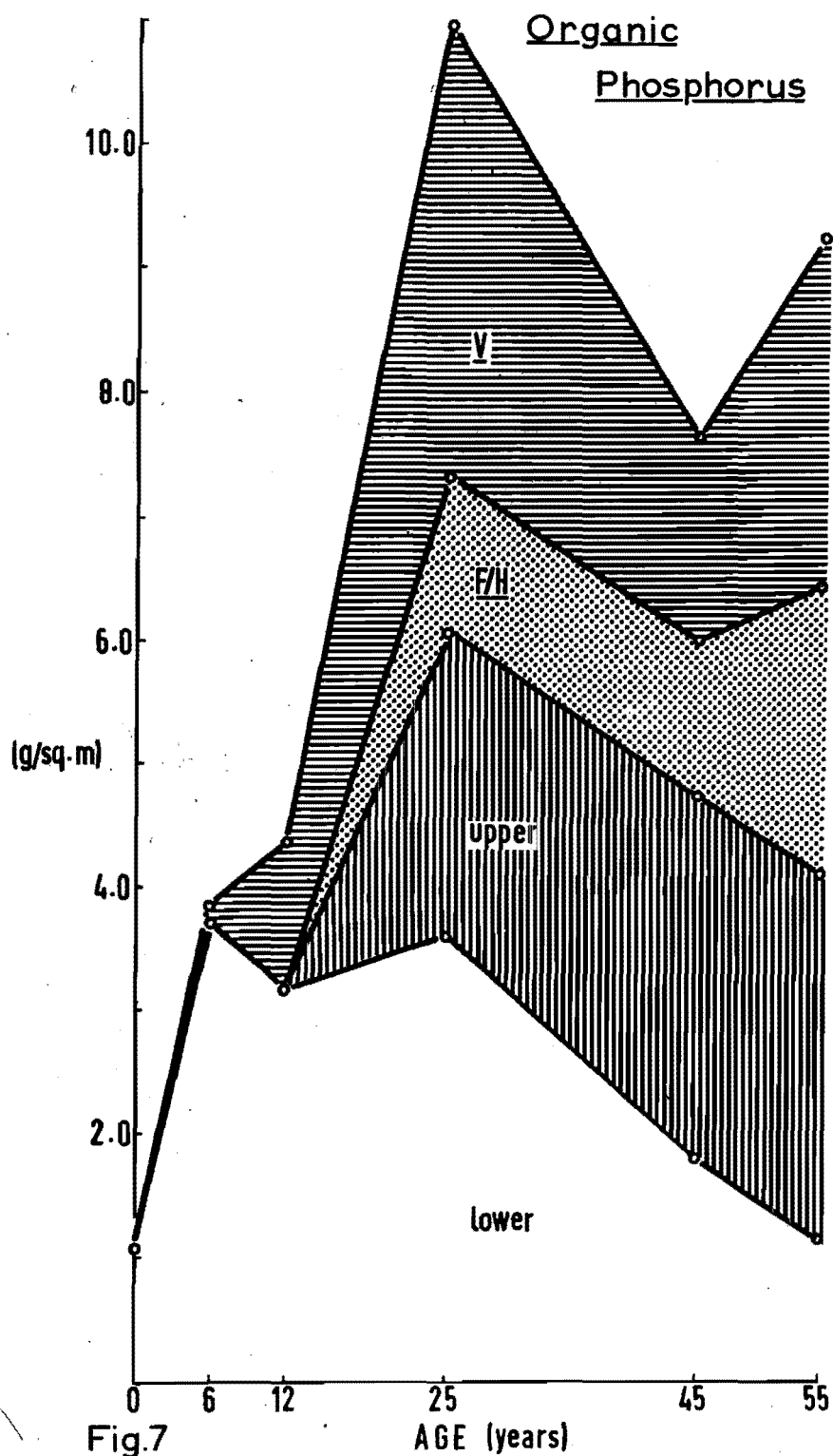
Table 11..

Organic Phosphorus.

(Mean values of 3 pits per Stage)

(All values expressed as  $\text{g/m}^2$ )

Stage	Upper Horizon	Lower Horizon	$\frac{F}{H}$	<u>V</u>		Upper + Lower		Upper+Lower+ $\frac{F}{H}$		Ecosystem	
				%P	( $\text{g/m}^2$ )		% $P_o$ of $P_t$		% $P_o$ of $P_t$		% $P_o$ of $P_t$
I	1.07	-	-	-	-	1.07	2.2	1.07	2.2	1.07	2.2
II	3.69	-	-	0.068	0.15	3.69	5.9	3.69	5.9	3.84	6.1
III	3.16	-	-	0.068	1.20	3.16	4.5	3.16	4.5	4.36	6.2
IV	2.47	3.61	1.26	0.066	3.64	6.08	6.5	7.34	7.8	10.98	11.4
V	2.94	1.82	1.26	0.048	1.65	4.76	7.8	6.02	9.5	7.67	11.8
VI	2.97	1.16	2.34	0.035	2.82	4.13	6.2	6.47	10.0	9.29	14.3



## III. 6 ORGANIC PHOSPHORUS.

See Table 11 and Figure 7. Detailed figures are in Appendix III (f).

1. The regressions are:

$$\text{Ecosystem: } y = 3.11 + 0.130 x \quad (r = 0.790)$$

$$\text{Upper+Lower+}\underline{\text{F/H}}: y = 2.61 + 0.085 x \quad (r = 0.792)$$

$$\text{Upper+Lower: } y = 2.77 + 0.044 x \quad (r = 0.581)$$

The correlation coefficients are not good, especially in Upper+Lower. These regressions and their correlations would be better if Stage IV were excluded.

2. There is a general accumulation of  $P_o$ , at the rate of  $0.130 \text{ g/m}^2/\text{annum}$  in the Ecosystem. The rate of accumulation in Upper+Lower+F/H is  $0.085 \text{ g/m}^2/\text{annum}$ .

3. There is very little  $P_o$  in Stage I.

4. The large amounts of  $P_o$  in Stage IV are a reflection of the heavy weights of V and F/H, and also one pit (pit 3), which has a large amount of fine mineral material. The effect is less pronounced if p.p.m. values are considered.

5. The decline of  $P_o$  in Upper plus Lower horizons from Stages IV to VI may or may not be a real effect.

6. There is a steady increase in the percentage of  $P_o$  in the Upper+Lower+F/H from 2.2% to 10.0%. This is not high compared to levels attained in mature grassland soils (in some cases, over 80% (Walker and Adams, 1958)), but is interesting considering the youth of the soils.

7. The P in the vegetation has been regarded as wholly organic, an assumption which may not be justified. In the presence of

Table 12..

## The "Coriaria" Pit.

	Weight (g/m <sup>2</sup> )	pH	Organic carbon		Nitrogen		Phosphorus (parts per million)		Phosphorus (g/m <sup>2</sup> )		Organic Phosphorus (g/m <sup>2</sup> )	%P <sub>o</sub> of P <sub>t</sub>
			%C	(g/m <sup>2</sup> )	%N (g/m <sup>2</sup> )	P <sub>t</sub>	P <sub>a</sub>	P <sub>t</sub>	P <sub>a</sub>			
Pit - fines less than 2 mm.	75,100	6.89	0.29	218	0.03	22.5	769	736	57.8	55.3	2.5	4.3
Silt on surface	4650	6.38	1.08	50	0.05	2.3	1245	1069	5.8	5.0	0.8	13.8
MINERAL MATTER:-				268		24.8			63.6	60.3	3.3	5.2
Vegetation	2170		15.37	334	0.56	12.2			1.6		1.6	
ECOSYSTEM				602		37.0			65.2	60.3	4.9	7.5

an ample supply of P, plants will extract luxury amounts of  $P_a$  from the soil, and some of this may remain in the inorganic form within the plant. It has, however, entered the organic cycle. The %P in the V falls during the sequence, which may indicate that less P is being taken up by the plants, or that the tree species of Stage VI do not require as much P as the Carmichaelia of Stages II, III and IV.

### III. 7 THE "CORIARIA" PIT.

See Table 12.

1. The age of the surface where this pit was dug is rather indeterminable, but is probably only a couple of years. It is not likely to be older than five or six years. Therefore, if this pit is compared with Stage II, some interesting differences are noted. The surface silty material was fine micaceous glacial flour, trapped by the Raoulia mat under the Coriaria plant. The weight of the V includes some of this silt, so is not a reliable figure.

2. pH is rather lower than would be expected, especially in the silt.

3. Organic C has accumulated rather faster than in Stage II.

4. The %N in the vegetation was higher than in similar material of Stage II (0.56% compared with 0.33%), and the accumulation of N appears to have proceeded at a very rapid rate. Allowing for  $8.7 \text{ g/m}^2$  of N in the PM (Stage I), the amount of N in the soil ( $24.8 \text{ g/m}^2$ ) is much greater than that in Stage II ( $12.5 \text{ g/m}^2$ ). The increases are 16.1 and  $3.8 \text{ g/m}^2$  respectively;

accumulation occurs over four times faster, assuming that this pit is the same age as Stage II. If younger, the annual increments are much higher:  $8 \text{ g/m}^2$  (over 70 lb/ac) if only two years old. If the whole Ecosystem is considered, there has been an increase in two years of over  $28 \text{ g/m}^2$ ;  $14 \text{ g/m}^2/\text{annum}$  or 125 lb/ac/annum. This is about twice the highest rate of accumulation under Carmichaelia.

5. Levels of  $P_o$  may be slightly higher than Stage II, but probably not significantly so.  $\%P_o$  in the soil is the same as Stage II. An interesting effect is the high p.p.m. levels of  $P_t$  and  $P_a$  (and the large  $\%P_o$ ) in the surface silt. This may be due to the inclusion of fine Raoulia roots in this material, and there could also be less quartz in this glacial flour than in the sub-2mm morainic fines, and thus higher levels of P.

### III. 8 RATIOS OF CARBON, NITROGEN AND ORGANIC PHOSPHORUS.

See Table 13. Detailed values are in Appendix III (g).

1. C, N and  $P_o$  have been shown to accumulate in OM at rates such that the ratio C : N :  $P_o$  is very approximately 100 : 10 : 1. C/N ratios in productive grassland soils are usually near 10-12, C/ $P_o$  ratios might be expected to roughly approximate 100, and N/ $P_o$  ratios perhaps 10. The departures from these ratios in the Franz Josef soils, undergoing rapid accumulation of OM, are interesting. Barrow (1961) has reviewed the problems of calculating element ratios, especially P, in soil OM. C/N, C/ $P_o$  and N/ $P_o$  ratios have been recalculated on the basis of N = 10.

Table 13..

Ratios of Carbon, Nitrogen and organic Phosphorus.

(Means of 3 pits per Stage)

Stage	Upper + Lower Horizons						Upper+Lower+F/H						Ecosystem					
	C/N	C/P <sub>o</sub>	N/P <sub>o</sub>	Recalculated*			C/N	C/P <sub>o</sub>	N/P <sub>o</sub>	Recalculated			C/N	C/P <sub>o</sub>	N/P <sub>o</sub>	Recalculated		
				C	N	P <sub>o</sub>				C	N	P <sub>o</sub>				C	N	P <sub>o</sub>
I	10.5	86	8.2	105	10	1.22	10.5	86	8.2	105	10	1.22	10.5	86	8.2	105	10	1.22
II	8.1	26	3.3	81	10	3.03	8.1	26	3.3	81	10	3.03	10.3	34	3.4	103	10	2.94
III	7.4	44	6.4	74	10	1.56	7.4	44	6.4	74	10	1.56	17.8	162	8.9	178	10	1.12
IV	12.4	115	8.7	124	10	1.15	15.1	187	11.6	151	10	0.86	27.2	337	12.2	272	10	0.82
V	14.6	237	16.1	146	10	0.62	15.6	280	17.8	156	10	0.56	23.0	413	17.9	230	10	0.56
VI	15.3	373	24.1	153	10	0.41	17.7	375	21.1	177	10	0.47	34.7	647	18.4	347	10	0.54
"CORIARIA"	10.8	81	7.5	108	10	1.33	10.8	81	7.5	108	10	1.33	16.3	123	7.5	163	10	1.33

\* Recalculated on basis of N = 10

2. C/N ratios widen considerably, as expected in forested soils. The narrow ratios in Stages II and III are due to the addition of plant material high in N from Carmichaelia. Afforestation in Stage IV induces widening ratios, especially if the whole Ecosystem is considered.

3. C/P<sub>0</sub> ratios fluctuate widely, but the mean ratios tend to widen. The narrow ratios in Stages II and III are probably due to the rapid growth of a legume and the incorporation into the soil of OM from a plant requiring large amounts of P. The reverse situation probably applies from Stages IV to VI, where trees are growing and return of P<sub>0</sub> to the soil is relatively smaller. However, the previous assumption that all P in the V is organic may have affected the results; or, alternatively, release of P from the soil may not be fast enough to satisfy growth requirements.

4. N/P<sub>0</sub> ratios follow a similar trend.

5. The ratios of elements in the "Coriaria" pit show close similarity to Stage I in the Upper+Lower+F/H, and similarities to Stage III if the whole Ecosystem is considered. Values derived from just one pit are probably not very reliable, the inclusion of some silt (with the Raoulia) in the V may have affected the results.

### III. 9 EXTRA SOILS FROM THE FRANZ JOSEF REGION.

See Table 14.

1. The eight "grab" samples from the three older soils, tentatively styled "X", "Waiuta" and "Okarito" have been analysed,



and a comparison with the mean values of soil characteristics in Stage VI is both interesting and instructive. These extra samples may give some indication of the probable course of soil development after Stage VI. Their ages are quite indeterminate at the moment. Too much reliance should not be placed on the values, as sampling was rather rough and was not carried out on a volume-weight basis.

2. pH values show clear and consistent trends from Stage VI to "Okarito". Note the very low pH of "Okarito" "Litter/A", and the slight rise in pH of the "gley horizon" in "Waiuta".

3. Trends of %C are fairly consistent, though the marked decrease in "Waiuta" and "Okarito" litter samples is strange. Note that %C stays constant in upper horizons, but there is a drop in gley horizons. The "B" horizon of "Okarito" is probably the zone of humic accumulation in the podzol.

4. %N in the litter and upper horizons seems to decrease fairly consistently. Note the very low levels of N in the gley horizons. Bulk density of the soils probably increases throughout the sequence, but it is not possible to predict possible levels of N (in  $\text{g/m}^2$  or other quantitative measure) for soil or Ecosystem, as no estimations are available for the weight of N held in the aerial portions of the trees and other vegetation.

5. Trends in levels of  $P_t$ ,  $P_a$  and  $P_o$  are striking:  $P_t$  in litter, top and bottom horizons decreases markedly. The concentration of P in the litter or  $F/H$  shows the effect of the organic cycle, and it is possible that some leaching of P to lower horizons has occurred even at "Stage X", although some of the

loss from the top horizon is due to incorporation in growing vegetation.  $P_a$  likewise follows the same trend. Generally speaking,  $\%P_o$  increases through the sequence, although absolute levels of  $P_o$  are falling, along with  $P_t$  and  $P_a$ . Fairly high proportions of  $P_o$  are seen in the older soils, especially in the litter materials. Increasing  $\%P_o$  in the lower horizons is evident, but the low general levels of these proportions are probably due to the peculiar nature of forest soils compared to grassland soils. The tree roots ramify largely in the uppermost soil horizons, and there is only a slow turn-over of nutrients in the organic cycle. Most  $P_o$  will be held in the litter on the surface, and relatively more  $P_a$  may be leached into lower horizons. This might explain the high proportions of  $P_o$  in the litter layers, and the low proportions in lower horizons.

Table 14..

Extra Soils from the Franz Josef region.

(Mean values for the 3 pits of  
Stage VI included for comparison.)

Soil		LOI%	pH	%C	%N	P <sub>t</sub>	P <sub>a</sub>	P <sub>o</sub>	%P <sub>o</sub> of P <sub>t</sub>
						(ppm)	(ppm)	(ppm)	
Stage VI	<u>F/H</u>	56.9	5.54	29.05	1.325	1080	430	650	60.2
	Upper horizon	-	5.29	3.51	0.222	643	517	126	19.6
	Lower horizon	-	5.45	0.89	0.060	727	709	18	2.5
"Stage X"	Litter	62.49	4.16	32.66	1.297	913	250	663	72.6
	"A"	-	4.62	2.48	0.132	451	296	155	34.4
	"Gley horizon"	-	4.63	0.42	0.025	728	666	62	8.5
"Waiuta"	Litter	11.91	4.28	6.57	0.298	274	135	139	50.7
	"A"	-	4.32	3.14	0.159	202	129	73	36.1
	"Gley horizon"	-	5.30	0.97	0.040	310	213	97	31.3
"Okarito"	"Litter/A"	36.15	3.94	5.71	0.471	273	106	167	61.2
	"B"	-	4.61	3.09	0.086	166	101	65	39.2

## V. GENERAL DISCUSSION.

### V. 1 SAMPLING PROCEDURE.

#### V. 1 (1) PROBLEMS OF SITE SELECTION.

The prior recognition of the plant succession, and the areas upon which the plant communities were growing, greatly reduced the difficulties of selecting pit-sites. These areas were small (generally not larger than a hectare), and in most cases the communities were fairly homogenous. All these factors aided selection immensely, but there was still a wide range of sites available for sampling at each Stage. The basic principles which guided the choice of pit position have previously been mentioned (Section III. 1), and these were followed as much as possible. As the weights of F/H and V indicate (Section IV. 1), variability between pits of any Stage was certainly achieved, and some measure of the extremes of nutrient accumulation was gained. However, there were also unintentional variations in the volume-weights of fines in Upper and Lower horizons, and these have unduly affected the results. The primary difficulty with sampling soils on glacial moraines is the extreme stoniness of the ground, and more refined methods of sampling must be evolved to minimise these difficulties. The matter will be further discussed later.

Some preliminary samples taken in 1961 on surfaces which approximated to Stages II and IV established that differences

between Stages were likely to be much greater than differences between pits of any one Stage. The foregoing results have also shown this, although naturally there is some overlap between the highest and lowest extremes of successive Stages. Three pits were dug per Stage because it was thought that fewer pits would not provide reliable analytical figures, and more pits would prove too laborious a task when sampling. Another and better approach is to increase the cubic extent of the pit - "enlarging the Ecosystem". This is probably a more accurate method, if indeed 'accuracy' is possible when sampling such a heterogenous natural entity as a developing forest community, compared with a pasture on agricultural land. A larger pit would also reduce the errors in volume estimation caused by the boulders protruding into the pit from outside the specified soil Ecosystem. It would enable a more representative selection of plant species to be made, rather than a choice of only one or two species within the metre-square frame. However, it may not be desirable to aim for maximum variability of plant growth between pits. This is not always possible, as is shown by the weights of V from Stages V and VI. Maximum variability was desired in both, but only achieved in Stage VI. It appears that the plant community on Stage V is inherently homogenous. It is probable that the trend of ecological succession towards a climax vegetation is also towards greater uniformity of plant cover. The disproportionate influence of Stage IV on the volume-weights of nutrients (vide Figures 6 and 7) is disturbing, in that it tends to interrupt the even progression of nutrient accumulation throughout the sequence. It is entirely possible that an

unfortunate and non-representative choice was made when selecting pit-sites for this Stage. However, the effect could be a real one; growth of vegetation on this Stage is uniformly dense, stalks are close together and there are few clearings in the forest growth, which is not tall enough to inhibit the entry of light to all strata of the community. The character of plant growth changes markedly at Stage V; the trees are three or more metres taller and the Carmichaelia is etiolated and struggling for light. Its elimination at this Stage is probably due mainly to superior competition for light by other species. By Stage VI the character of the forest has again changed, and light has been so restricted by the growth of a dense canopy that shade-loving plants are common in the lower strata. The effects of these ecological changes cannot be divorced from the course of soil development, and the results obtained in this investigation seem to show the profound effects of floral and habit changes throughout the Chronosequence. These have an important influence on the operation of the organic cycle. Divergent ecological lines of succession in communities of older soils may be expected to exert a similar important influence on soil characteristics, so that surfaces of the same age may develop quite different soils. Any future work on the older soils will be greatly concerned with this factor.

#### V. 1 (2) THE METHOD OF SAMPLING.

In several ways the method of sampling soils in this work is superior to methods employed in earlier studies.

Firstly, the whole Ecosystem has been sampled, and has been divided into portions so that the distribution of nutrients between the soil, vegetation and the F/H layer could be studied. Secondly, a more representative soil sample has been obtained by the excavation of a pit big enough to minimise the effects of large boulders and preclude the exclusive sampling of small patches of abnormally fine mineral material. The pits were not large enough to ensure truly representative soil samples, but some success was achieved. In this respect, the use of a larger pit is advised. However, the method definitely has some faults, one of which is the vexatious problem of achieving a true volume-weight of mineral matter. All stones larger than  $\frac{1}{4}$ " were discarded at the pit, on the assumption that they are inert in plant nutrition during a short period of time. If they had been weighed, and samples analysed, a more accurate assessment of volume-weights, bulk densities and nutrient contents could have been made. However, the inclusion of large amounts of P from the boulders in each pit would have reduced to insignificance the small amounts of  $P_0$  which were detected. On the other hand, a more profitable approach would be the further sieving of the mineral matter before grinding, so that several particle size fractions could be analysed separately. It would be found that the finest fraction exhibited a much larger accumulation of  $P_0$  than has been recorded for these soils (Williams and Saunders, 1956a). Weathering of the coarser mineral fractions is extremely slow, and they probably take little part in plant nutrition during the youthful stages of soil development. Generally speaking,

those pits with heavy volume-weights of sub-2mm. mineral material also showed the greatest content of  $P_o$ .

The chief problem encountered was the identification of areas with an "intermediate" proportion of fines and boulders (Plate 4a). The visual appearance of the surface (in Stages I, II and III) was not necessarily indicative of the sub-surface conditions. In the other three Stages the problem was even more acute, as the surface was here disguised by a thick F/H layer. No satisfactory solution seems possible, except by the excavation of large numbers of pits and the subsequent selection of only the most representative. This is certainly not very practical.

Further work on older soils will also have to solve the difficulties of sampling the aerial portion of the Ecosystem. Ecological and forestry methods of assessing species and canopy density, timber growth, and other forest characteristics will have to be adapted to allow the most accurate estimation of nutrient content in this portion of the Ecosystem. Obviously, it will no longer be possible to remove the entire vegetal growth from a small area for weighing and analysis.

## V. 2      COMPARISON WITH PREVIOUS CHRONOSEQUENCE STUDIES.

The only comparable investigations are those of Crocker, Major and Dickson in Alaska and California. Mention has been made of these in the Review of Literature (Section II. 1 (3)), and they have been compared and contrasted with each



other. The present study will be discussed in relation only to the two Alaskan investigations, at Glacier Bay and Herbert/Mendenhall Glaciers.

The most striking feature of the three glacier recession studies is that the similarities between them are much more numerous than the differences. Although the Alaskan work embraced longer Chronosequences, and more soil characteristics were investigated, the similarities of the three sequences over the first half-century may perhaps be noted:

1. The similar natural features of the areas presented superb opportunities for ensuring constancy of the other four soil forming factors.
2. The climates in the three areas broadly resemble each other.
3. It was possible to accurately determine the ages of the soils.
4. Similar plant successions were recognised. These were all initiated by a patchy distribution of apparently non-N-fixing pioneers, followed by plants with known ability to fix atmospheric N, such as Alnus, Carmichaelia, Coriaria, Dryas and Shepherdia. All successions were characterised by the eventual elimination of the principal N-fixer ("the transition stage"), and the growth of a sub-climax forest containing conifers or similar species. The elimination of Alnus or Carmichaelia seems to be the result of competition for light by taller and dense canopied trees.
5. There was great difficulty with sampling, due to the more

or less bouldery and stony substrate. Special sampling methods had to be employed, with variable success.

6. Apparent "steady-states" of equilibrium of most soil characteristics were not achieved during the first half-century.

7. Mineralogical weathering had scarcely commenced, and differentiation of soil horizons (excepting by near-surface accumulation of OM) had not occurred.

8. The observed changes in various soil characteristics were mainly dependent upon the growth of plants and subsequent return of OM to the soil. The amount and type of OM governs many soil characteristics.

9. There is an areal pattern of soil formation which partially reflects the areal pattern of pioneer plant establishment.

10. All three Chronosequences are characterised by large increases in amounts of OM, N and organic C; by the initiation of nutrient gradients between the surface and sub-surface layers of the soil; and by the decline in pH levels of mineral soil and forest floor.

The small differences that were observed between the Glacier Bay and Herbert/Mendenhall areas, and even between Herbert and Mendenhall sequences, are attributable to small but significant differences in one or more of the soil forming factors other than Time. For instance, pH values attained lower levels at Herbert/Mendenhall than at Glacier Bay, due partly to a wetter climate but mainly to the more basic PM of the latter sequence, combined with a slower rate of plant colonisation. The climate

at Mendenhall was more favourable for vegetal growth than at Herbert, and larger amounts of organic C accumulated. Crocker and Dickson mentioned other differences, but the impossibility of ensuring strict similarity between sequences does not however invalidate comparison. Table 15 shows the amounts of C, N and OM accumulated in the three areas over 45-55 years, and their annual increments. The soils at Glacier Bay were mostly sampled to 18", at Herbert/Mendenhall generally to 24", and those at Franz Josef to 13" (33cm.). The glacial till was apparently rather finer in Alaska than at Franz Josef. An abrupt decrease in the annual increments of N is reported after the Alnus disappears in Alaska (70-100 years), but the Franz Josef sequence was too young to properly observe any diminution in the rate of N accumulation.

It is apparent that the soils at Franz Josef are not accumulating C, N and OM in mineral soil and F/H as fast as the other sequences, probably because the coarser substrate tends to restrict plant growth. Alnus is probably a more effective N-fixer than Carmichaelia, whose litter return is meagre. Coriaria, which appears to be the Southern Hemisphere analogue of Alnus, certainly fixes more impressive amounts of N than Carmichaelia in this region, but the figures in Section IV.7 are not very reliable and valid comparisons with Glacier Bay and Herbert/Mendenhall cannot be made.

The analytical figures for  $P_t$ ,  $P_a$  and  $P_o$  have been discussed at some length in the relevant sections (IV.5 and IV.6) and again in V.1 (2). Neither of the Alaskan studies mentioned the importance of P in OM accumulation, but P certainly cannot have been lacking considering the rates of OM accumulation reported for those Chronosequences. Walker and Adams (1958) have proposed competition for P as a major factor limiting legume growth in grass-clover associations, where  $P_o$  may be greater than 80% of the  $P_t$ . At Franz Josef,  $P_o$  in the sub-2mm. fraction has not exceeded 10%, but this could still be a big factor if  $P_a$  is too slowly available because of large particle size. Organic phosphorus could, however, be a large proportion of the very finest fractions of mineral matter, which may be the only fraction the plants draw upon for their nutrients. The high C/ $P_o$  ratios in Stages V and VI suggest a deficiency of P. It appears, therefore, that the suppression of Carmichaelia after Stage V may be due to two factors: the competition for light, and the insufficient supply of P. The former is probably the most important.

It will be of great interest to determine whether total N in the Ecosystem continues to increase in older soils. If this occurs in the absence of Carmichaelia or other known N-fixer, N-fixation by free-living micro-organisms in the soil or phyllosphere must have taken place. Another possibility is N fixation by Coprosma and many other species, as postulated by Stevenson, and it is important that this work be checked.

Table 15..

A Summary of Nutrient Accumulation in three Chronosequences.

(Values given are for Soil plus Forest Floor only.)

	<u>Total N</u>	<u>Annual increment</u>	<u>Total C</u>	<u>Annual increment</u>	<u>Dry matter of surface litter layers</u>	<u>Annual increment</u>
	(g/m <sup>2</sup> )	(g/m <sup>2</sup> /annum)	(g/m <sup>2</sup> )	(g/m <sup>2</sup> /annum)	(g/m <sup>2</sup> )	(g/m <sup>2</sup> /annum)
<u>Glacier Bay</u> (45 years)	280	6.2	3700	82	5000+	100+
<u>Herbert/ Mendenhall</u> (50 years)	200	4.0	4000	80	4000+	80+
<u>Franz Josef</u>	130	2.4	2300	41	3600	65

## V. 3            PROFITABLE TOPICS FOR FUTURE INVESTIGATIONS.

There are a number of fascinating problems for the soil scientist in this area. A few may be mentioned, giving an indication of future lines of enquiry:

1. More information is needed on the sources of N in the pioneer communities. It is probable that plant requirements are small, and may be satisfied by accessions from rain, river water and growth of micro-organisms, but this is not certain. Long-term rain collections would give some measure of the importance of this N source. Isotopic N studies with some of the pioneer plants, such as mosses and Gunnera albocarpa, should establish whether they are able to fix atmospheric N. Similarly, the work of Stevenson on Coprosma, Griselinia and other species should be confirmed or disproved.

2. The role of Coriaria as a sub-pioneer should be investigated by reliable methods of sampling. The probable importance of this plant should be thoroughly elucidated.

3. Methods of sampling should be developed to gauge the effect of Carmichaelia plants on surrounding species. The decreasing vigour of Olearia seedlings growing at increasing radial distances from the Carmichaelia plant is striking. It should be possible to statistically demonstrate a diminution of influence on these plants by the "nurse" species.

4. An interesting approach to the problem of variability within any Stage might be made by extensive sampling of one Stage. The use of statistical techniques would aid in the randomisation of pits and allow the formulation of basic

principles for sampling stony forested soils.

5. Mineralogical studies should be made on the soils of the sequence, and of older soils. These would possibly enable some measure of weathering rates and clay formation in these coarse PM's.

6. Further elucidation of the soil forming processes will await the determination of other soil characteristics, such as C.E.C., exchangeable cations and total elements such as Ca, Mg, K, Na, Fe, Al, Si, etc. A detailed fractionation of inorganic Phosphorus would provide further information.

7. The inability of the present study to demonstrate the attainment of apparent "steady-states" in soil properties was not unexpected, and further sampling of older soils is proposed. Fortunately, a botanical succession may be recognised, and there are some hopes of tracing the course of soil development past these juvenile soils; studying nutrient accumulation, equilibrium and eventual loss from the Ecosystem. Soil development on the West Coast, under an immense rainfall, cannot but lead to ultimate degradation to infertile soils such as podzols, which is indeed the case. If it is possible to estimate surface age and to keep relief, PM, climate and biotic factor constant (or ineffectually varying) over a range of older soils, a true picture may be formed of the "birth, life and death" of a West Coast soil. The prospects are encouraging and exciting.

## VI.

SUMMARY.

1. A Chronosequence of soils and vegetation on the recessional moraines of the Franz Josef Glacier in South Westland was recognised, described and investigated.

2. An extensive Review of the literature pertaining to Chronosequences, soil/plant co-development studies, and the accumulation of Nitrogen in soils was made.

3. A method of sampling coarse bouldery soils on a volume-weight basis was developed.

4. The accumulation of Carbon, Nitrogen, and organic Phosphorus was studied. After 55 years the Ecosystem contained  $5.8 \text{ kg/m}^2$  organic Carbon,  $169 \text{ g/m}^2$  Nitrogen and  $9 \text{ g/m}^2$  organic Phosphorus. C/N ratios widened from 10.5 to 34.7 throughout the sequence, and percentage organic Phosphorus increased from 2.2 to 14.3. The mineral soil plus forest floor (F/H) contained  $2.3 \text{ kg/m}^2$  organic Carbon,  $130 \text{ g/m}^2$  Nitrogen and  $6.5 \text{ g/m}^2$  organic Phosphorus. C/N ratios in this portion of the Ecosystem increased from 10.5 to 17.7, and percentage organic Phosphorus increased from 2.2 to 10.0.

5. Reaction of the upper few centimetres of mineral soil decreased from 7.89 to 5.29 in 55 years. The lowest value recorded was 4.96.

6. A single Coriaria plant and underlying soil was sampled and similarly treated. Accumulation of Nitrogen in the soil



occurred at least four times faster than under Carmichaelia, and the highest rate of increase was probably not less than 14 g/m<sup>2</sup> (125 lb/ac) per annum in the Ecosystem.

7. Some older soils from the Franz Josef region were sampled on a non-volume-weight basis and the probable course of soil development discussed. Soil pH decreased to approximately 4.0; amounts of total Phosphorus and inorganic Phosphorus in the mineral soil decreased markedly from near 700 p.p.m. to 160 and 100 p.p.m. respectively, and the percentage organic Phosphorus increased, although absolute amounts probably decreased.

8. Similarities and differences between this Chronosequence and others on glacial moraines in Alaska were discussed. The rates of accumulation of Carbon and Nitrogen, and the levels attained, were lower at Franz Josef than in Alaska.

9. The method of sampling employed was criticised and improvements considered. Further profitable topics for investigation were suggested.

10. The preliminary results of microbiological studies by Dr. M. di Menna and Dr. E.A. Flint of the Soil Bureau were presented in Appendices IV and V. These further elucidated the biotic conditions existing within the soils and their parent materials.

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REFERENCES.

- ALLEN E.K., ALLEN O.N. (1958) Biological aspects of symbiotic N fixation.  
 Encycl. Plant Physiol. 8, 48-118.  
 Ruhland, W.; Ed., Springer-Verlag.  
 Berlin.
- ALLISON F.E. (1955) The enigma of soil N balance sheets.  
 Adv. Agron. 7, 213-250.
- ALLISON F.E., GADDY V.L., PINCK L.A., ARMINGER W.H. (1947)  
 Azotobacter inoculation of crops.  
 I. Historical.  
 II. Effect on crops under greenhouse conditions.  
 Soil Sci. 64, I. 413-430  
 II. 489-498.
- ALLISON F.E., HOOVER S.R. (1935)  
 Conditions which favour N fixation  
 by a blue-green alga.  
 Trans. 3rd Int. Cong. Soil Sci.  
I 145-147.
- ATKINSON I.A.E. (1959) Soils and the growth of Pinus radiata at Cornwallis, Auckland.  
 N.Z.J.Sci. 2 443-472.
- BARRETT B.C. (1961) Pollen analysis and the time factor in pedogenesis.  
 Soil News 1961 (6) 251-256.
- BARRETT B.C. (1962) Soil organic regime of coastal sand dunes.  
 Nature 196, 835-837.
- BARROW N.J. (1961) Phosphorus in Soil Organic Matter.  
 Soils and Fertilisers 24, (3),  
 169-173
- BAYLIS G.T.S. (1959) Effect of vesicular-arbuscular Mycorrhizas on growth of Griselinia littoralis (Cornaceae).  
 New Phytol. 58, 274-280.
- BAYLIS G.T.S. (1961) The significance of mycorrhizas and root nodules in New Zealand vegetation.  
 Proc. Roy. Soc. N.Z. 89 (1)  
 45-50.

- BAYLIS G.T.S. (1962) Personal communication.
- BEADLE N.C.W. (1953) - The edaphic factor in plant ecology with a special note on soil phosphates.  
Ecol. 34 (2) 426-428.
- BEADLE N.C.W. (1954) Soil phosphate and the delimitation of plant communities in Eastern Australia.  
Ecol. 35 370-375
- BEADLE N.C.W. (1962a) Soil Phosphorus and the delimitation of plant communities in Eastern Australia.  
Ecol. 43 281-288
- BEADLE N.C.W. (1962b) An alternative hypothesis to account for the generally low phosphate content of Australian soils.  
Aust. J. Ag. Res. 13 434-442.
- BEADLE N.C.W., BURGESS A. (1949)  
Working capital in a plant community.  
Aust. J. Sci. 11 207-208
- BEADLE N.C.W., Y.T. TCHAN (1955)  
Nitrogen economy in semi-arid plant communities.  
I. The environment and general considerations.  
II. The non-symbiotic N-fixing organisms.  
Proc. Linn. Soc. N.S.W. 80  
I. 62-70  
II. 98-104
- BELL, J. Mackintosh, (1910); with R.P. GREVILLE, L. COCKAYNE.  
"A geographical report on the Franz Josef Glacier."  
New Zealand Department of Mines.  
Geological Survey.
- BILLINGS W.D. (1941) Quantitative correlations between vegetational changes and soil development.  
Ecol. 22 448-456.
- BILLINGS W.D. (1952) The environmental complex in relation to plant growth and distribution.  
Quart. Rev. Biol. 27 251-265
- BOND G. (1955) An isotopic study and the fixation of Nitrogen associated with nodulated plants and Alnus, Myrica and Hippophae.  
J. Expt. Bot. 6 303-312.
- BOND G. (1956) Evidence for the fixation of Nitrogen by root nodules of Alder (Alnus) under field conditions.  
New Phytol. 55 147-153.

- BOND G. (1957a) The development and significance of the root nodules of Casuarina.  
Ann. Bot. Lond. NS 21 373-380
- BOND G. (1957b) Isotopic studies of Nitrogen fixation in non-legume root nodules.  
Ann. Bot. Lond. NS 21 513-522
- BOND G. (1958a) "Symbiotic Nitrogen fixation by non-legumes".  
in "Nutrition of legumes" - ed. by  
E.G. Hallsworth. p. 216-231  
Proc. Easter school of Ag. Sci.  
Nottingham. 1958.
- BOND G. (1958b) Root nodules of Coriaria.  
Nature 182 474-475
- BOND G. (1959) "Fixation of Nitrogen in non-legume root nodule plants." in Symposia of the Soc.  
for Expt. Biol. (XIII.) p. 59-71.  
Cambridge U.P.
- BOND G., FLETCHER W.W., FERGUSON T.P. (1954)  
The development and function of the root nodules of Alnus, Myrica and Hippophae.  
Plant and Soil. 5 309-323.
- BOND G., SCOTT G.D. (1955)  
An examination of some symbiotic systems for the fixation of Nitrogen.  
Ann. Bot. Lond. NS 19 67-78
- BRAUN-BLANQUET J., JENNY H. (1926)  
Vegetationsentwicklung und Bodenbildung in der alpinen Strufe der Zentralpen.  
Neue Denkschr. Schweiz. Naturf. Ges.  
63 175-349. (Original not seen.)
- BRODRICK T.M. (1906) On the retreat of the Glaciers.  
Appendix to the Journal of the House of Representatives of New Zealand.  
Session II C-19 App. 2. 16-17.
- BUCHANAN G., from P. and G. GRAHAM (1951)  
The movements of the Franz Josef Glacier.  
N.Z. Alpine J. 13 123-125
- BURGES A., DROVER D.P. (1953)  
The rate of podzol development in sands of the Woy-Woy district, N.S.W.  
Aust. J. Bot. 1 83-94.
- BUTLER B.E. (1956) Parna - an aeolian clay.  
Aust. J. Sci. 18 145-151

- BUTLER B.E., HUTTON J.T. (1956)  
Parna in the Riverine plain of South Eastern Australia and the soils thereon.  
Aust. J. Ag. Res. 7 536-553.
- BUTLER G.W., BATHURST N.O. (1956)  
The underground transference of N from clover to associated grass.  
Trans. 7th Int. Gr. Cong. 168-178
- CAMERON R.E., W.H. FULLER (1960)  
Nitrogen fixation by some algae in Arizona soils.  
Proc. Soil Sci. Soc. Am. 24 353-356.
- CHANDLER R.F. (1938) Cation exchange properties of certain forest soils in the Adirondack section.  
J. Agric. Res. 59 491-505.
- CHANDLER R.F. (1942) The time required for podzol profile formation as evidenced by the Mendenhall glacial deposits near Juneau, Alaska.  
Proc. Soil Sci. Soc. Am. 7 454-459.
- CHAVASSE C.G.R. (1962)  
Forests, Soils and Landforms of Westland.  
N.Z. Forest Service Information Series. Bulletin No. 43.
- CLEMENTS F.E. (1916) "Plant Succession"  
Carnegie Inst. of Washington.
- COALDRAKE J.E., HAYDOCK K.P. (1958)  
Soil phosphorus and vegetal pattern in some natural communities of South East Queensland, Australia.  
Ecol. 39 1-5.
- COALDRAKE J.E. (1962) The Nitrogen of natural plant communities.  
in CSIRO Tropical Pastures Symposium. p.35.
- COCKAYNE L. (1927) New Zealand plants and their story.  
N.Z. Board of Science and Art.  
Manual 6 3 ed. N.Z. Government Printer.
- COCKAYNE L. (1928) "Vegetation of New Zealand."  
H.R. Engelmann (J. Cramer)  
Reprint 1958 of 2ed. pp 456.
- COILE T.S. (1940) Soil changes associated with loblolly pine succession on abandoned agricultural land of the Piedmont plateau.  
Duke Univ. Sch. Forestry. Bull. 5  
Durham, N. Carolina.

- CONNOR H.E. (1959) "Something about Plants"  
in Mount Cook National Park Handbook.  
 pp. 64. Printed by Wright and Carman  
 Ltd., Wellington.
- COOKE W. Bridge, LAWRENCE D.B. (1959)  
 Soil Mould fungi isolated from recently  
 glaciated soils in South Eastern Alaska.  
 J. Ecol. 47 529-549
- COOPER R., RUDOLPH F.D. (1953)  
 The role of lichens in soil formation and  
 plant succession.  
 Ecol. 34 805-807.
- COOPER W.S. (1923a) The recent ecological history of Glacier Bay,  
 Alaska.  
 I. The Interglacial forests of Glacier Bay.  
 Ecol. 4 93-128.
- COOPER W.S. (1923b) The recent ecological history of Glacier Bay,  
 Alaska.  
 II. The present vegetation cycle.  
 Ecol. 4 223-246
- COOPER W.S. (1923c) The recent ecological history of Glacier Bay,  
 Alaska.  
 III. Permanent quadrats at Glacier Bay. An  
 initial report.  
 Ecol. 4 355-365
- COOPER W.S. (1924) The forests of Glacier Bay - present, past  
 and yet unborn.  
 J. Forestry. 22 16-23.
- COOPER W.S. (1925) The recent ecological history of Glacier Bay,  
 Alaska. Ecol. 6 197.
- COOPER W.S. (1931) A third expedition to Glacier Bay, Alaska.  
 Ecol. 12 61-95.
- COOPER W.S. (1937) The problem of Glacier Bay, Alaska; a study  
 of glacier variations.  
 Geogr. Rev. 27 37-62.
- COOPER W.S. (1939) A fourth expedition to Glacier Bay, Alaska.  
 Ecol. 20 130-155.
- COTTHAM G., CURTIS J.T. (1956)  
 The use of distance measures in  
 phytosociological sampling.  
 Ecol. 37 (3) 451-460



- COWIE J.D. (1962) The time factor in soils developed from wind-blown sands.  
Soil News 1962. (3) 143-145.
- COWLES H.C. (1899) The ecological relationships of the vegetation on the sand-dunes of Lake Michigan.  
Bot. Gaz. 27. 95-117, 167-202, 281-308, 361-391.
- CROCKER R.L. (1952) Soil Genesis and the Pedogenic factors.  
Quart. Rev. Biol. 27 (2) 139-168.
- CROCKER R.L. (1959) The plant factor in soil formation.  
Aust. J. Sci. 21 180-193.
- CROCKER R.L., DICKSON B.A. (1957)  
Soil development on the recessional moraines of the Herbert and Mendenhall Glaciers, SE Alaska.  
J. Ecol. 45 169-185.
- CROCKER R.L., MAJOR J. (1955)  
Soil development in relation to vegetation and surface age at Glacier Bay, Alaska.  
J. Ecol. 43 (2) 427-448.
- CROWTHER C., RUSTON A.G. (1911)  
The nature, distribution and effects upon vegetation of atmospheric impurities in and near an industrial town.  
J. Agric. Sci. 4 25-55.
- CSIRO DIVISION OF TROPICAL PASTURES (COMMITTEE OF) (1962)  
Symposium: "A review of Nitrogen in the tropics with particular reference to pastures." CAB., Alden Press. pp. 185.
- DAVIS J.H. (1940) The ecologic and geologic role of mangroves in Florida.  
Papers Tortugas Lab 32 303-412  
Carnegie Inst. Washington. Publ. 517. (Original not seen.)
- DELWICHE C.C., WIJLER J. (1956)  
Non-symbiotic Nitrogen fixation in soil.  
Plant and Soil 7 (2) 113-128.
- DICKSON B.A., CROCKER R.L. (1953-54)  
A Chronosequence of soils and vegetation near Mt. Shasta, California.  
I. Definition of the Ecosystem investigated and features of the plant succession.  
J. Soil Sci. 4 123-142.

- II. The development of forest floors and C/N profiles of the soils. ibid. 142-154.  
 III. Some properties of the mineral soils. ibid. 5 173-191.

- di MENNA M (1962) Personal communication.
- DOUGLAS C.E., HARPER A.P. (1895)  
 Report on the Westland Alps, New Zealand.  
 (from November 1893 to May 1894)  
 Geog. J. 5 61-68.
- ERIKSSON E. (1952) Composition of Atmospheric precipitation.  
 I. Nitrogen Compounds.  
 Tellus 4 215-232.
- ERIKSSON E. (1958) The chemical climate and saline soils of the arid zone.  
in "Climatology". UNESCO. p. 147-180
- FERGUSON T.P., BOND G. (1953)  
 Observations on the formation and function of the root nodules of Alnus glutinosa L. (Gaertn).  
 Ann. Bot. Lond. NS 17 175-188.
- FIELD W.O. (1937) Observations on Alaskan coastal glaciers in 1935.  
 Geogr. Rev. 27 37-62.
- FIELD W.O. (1947) Glacier recession in Muir Inlet, Glacier Bay, Alaska.  
 Geogr. Rev. 37 369-399.
- FISHER R.T. (1928) Soil changes and silviculture on the Harvard Forest.  
 Ecol. 9 6-11.
- FLEMING C.A. (1962) New Zealand Biogeography.. (A Paleontologist's Approach)  
 Tuatara 10 (2) 53-108.
- FLETCHER W.W. (1955) The development and structure of the root nodules of Myrica gale L. with special reference to the nature of the endophyte.  
 Ann. Bot. Lond. NS 19 501-514.
- FLINT R.F. (1959) "Glacial and Pleistocene Geology"  
 Wiley. New York.
- FLOATE M.J.S. (1962) Pedogenic relationships concerning forms of soil phosphorus and soil organic matter.  
 Ph.S. Thesis; deposited at King's College, Durham.

- GARNIER B.J. (1958) "The Climates of New Zealand"  
Edward Arnold (Publishers) Ltd.  
London. pp. 191.
- GAST P.R. (1937) Contrasts between the soil profiles  
developed under pines and under hardwoods.  
J. For. 35 11-16.
- GIBBS H.S., MERCER A.D., COLLIE T.W. (1950)  
Soils and Agriculture of Westland, New  
Zealand.  
Soil Bureau Bulletin No. 2 (NS)
- GOOD R.d'O. (1930) The geography of the genus Coriaria.  
New Phytol. 29 170-198.
- GORHAM E. (1953a) The development of the humus layer in some  
woodlands of the English Lake District.  
J. Ecol. 41 123-150.
- GORHAM E. (1953b) Chemical studies on the soils and vegetation  
of waterlogged habitats in the English Lake  
District.  
J. Ecol. 41 345-360.
- GRAY G. (1888) On the dissolved matter contained in rain-  
water collected at Lincoln, Canterbury,  
New Zealand.  
Proc. Aust. Ass. Adv. Sci. I 138-  
152.
- GRIFFITH B.G., HARTWELL E.W., SHAW T.E. (1930)  
The evolution of soils as affected by the  
old field white pine-mixed hardwood  
succession in Central New England.  
Harvard For. Bull. 15 pp. 82.
- GUNN B.M. (1960) Structural features of the Alpine Schists  
of the Franz Josef-Fox Glacier region.  
N.Z. J. Geol. Geophys. 3 287-308.
- HALLSWORTH E.G. (1958)  
"Nutrition of Legumes"  
Proc. 5th Easter School of Ag. Sci.  
at Nottingham. ed. E.G. Hallsworth.  
Butterworth Press.
- HANDLEY W.R.C. (1954) Mull and Mor formation in relation to forest  
soils.  
H.M.S.O. Forestry Commission Bull. 23.
- HANNON NOLA J. (1956) The status of Nitrogen in the Hawkesbury  
sandstone soils and their plant communities  
in the Sydney district.  
I. The significance and level of Nitrogen.  
Proc. Linn. Soc. N.S.W. 81 119-143.

- HANSON H.C., WHITMAN W. (1938)  
 Characteristics of major grassland types in  
 Western North Dakota.  
 Ecol. Monogr. 8 57-114.
- HARPER A.P. (1893) Exploration and character of the principal  
 New Zealand glaciers.  
 Geogr. J. 1 (1) 32-42.
- HARPER A.P. (1894) "Pioneer work in the Alps of New Zealand"  
 T. Fisher Unwin. London. pp.336.
- HARPER A.P. (1926) Variations of the Franz Josef glacier.  
 N.Z. Alpine J. III 343-349.
- HARPER A.P. (1934) Glacier retreat.  
 N.Z. Alpine J. 5 322.
- HARPER A.P. (1935) Glacier retreat.  
 N.Z. Alpine J. 6 173.
- HARPER A.P. (1946) "Memories of Mountains and Men"  
 Simpson and Williams, Christchurch.  
 pp. 208.
- HARPER A.P., DOUGLAS C.E. (1894)  
 On the Westland Alps. The Franz Josef  
 Glacier. (Reports of explorers for the  
 Dep't Lands & Survey)  
 Appendix to J. House Repts. N.Z.  
 No.1. C-1 App. 6 71-79.
- HARRADINE F., JENNY H. (1959)  
 Influence of Parent Material and climate on  
 texture and Nitrogen, Carbon contents of  
 virgin California soils.  
 I. Texture and Nitrogen Contents.  
 Soil Sci. 85 235-243.
- HARRINGTON H.J. (1951)  
 Glacier wasting and retreat in the Southern  
 Alps of New Zealand.  
 J. Glaciol. 2 140-145.
- HARRIS G.P., MORRISON T.M. (1958)  
 Fixation of Nitrogen by excised nodules of  
Coriaria arborea Lindsay.  
 Nature 182 1812.
- HEUSSER Calvin J. (1953)  
 Radiocarbon dating of the thermal maximum in  
 South East Alaska.  
 Ecol. 34 637-640.

- HISSINK D.J. (1938) The reclamations of Dutch saline soils (solonchaks) and their further weathering under humid climatic conditions of Holland. Soil Sci. 45 83-94.
- HOLLOWAY J.T. (1954a) An ecological classification of the Forest types of the Westland Podocarp region. N.Z. J. For. 7/1 23-33.
- HOLLOWAY J.T. (1954b) Forests and Climates in the South Island of New Zealand. T. Roy. Soc. N.Z. 82 (2) 329-410.
- HOLLOWAY J.T. (1959) The Pre-European Vegetation of New Zealand. in McIntock. 1959. Descriptive Atlas of New Zealand. N.Z. Gov't. Printer.
- HOLLOWAY J.T. (1962) The Forests of the South and the climatic change hypothesis. Paper given at meeting of the N.Z. Ecological Soc. at Gisborne. 1962. In press.
- HUTTON C.E. (1950) Chemical and physical properties of a chrono-litho-sequence of loess-derived soils in South West Iowa. Proc. Soil Sci. Soc. Am. 15 318-324.
- IKE J.F. jr, STONE E.L. (1958) Soil Nitrogen accumulation under Black Locust (Robinia pseudoacacia) Proc. Soil Sci. Soc. Am. 22 (4) 346-349.
- INGHAM G. (1950a) The mineral content of air and rain and its importance to agriculture. J. Agric. Sci. 40 55-61
- INGHAM G. (1950b) Effect of materials absorbed from the atmosphere in maintaining soil fertility. Soil Sci. 70 205-212.
- JANSEN H.S. (1962) Comparison between ring dates and C<sub>14</sub> dates in a kauri log. N.Z. J. Sci. 5 (1) 74-84.
- JENNY H. (1941) "Factors of Soil Formation" - A system of Quantitative Pedology. McGraw-Hill Book Company, Inc. New York and London. pp 281.

- JENNY H. (1946) Arrangement of soil series and types according to functions of soil forming factors.  
Soil Sci. 61 375-391.
- JENNY H. (1958) Rôle of the plant factor in the pedogenic functions.  
Ecol. 39 (1) 5-16.
- JENNY H. (1960) Comparison of soil Nitrogen and Carbon in temperate and tropical regions. (India and the Americas.)  
Miss. Ag. Exp. Station. Bull. 765.
- JENNY H. (1961) Derivation of State Factor equations of soils and Ecosystems.  
Proc. Soil Sci. Soc. Am. 25 (5) 385-388.
- JENSEN H.L. (1940) Contributions to the Nitrogen economy of Australian wheat soils, with particular reference to N.S.W.  
Proc. Linn. Soc. N.S.W. 65 1-112.
- JENSEN H.L. (1950) A survey of biological Nitrogen fixation in relation to the world supply of Nitrogen.  
Trans. 4th Int. Cong. Soil Sci. 1 1-8.
- JENSEN H.L., SWABY R.J. (1940) Further investigations on Nitrogen fixing bacteria in soil.  
Proc. Linn. Soc. N.S.W. 65 557-564.
- JUDD B.I., WELDON M.D. (1939) Some changes in the soil during natural succession of vegetation after abandonment in Western Nebraska.  
J. Am. Soc. Agron. 31 217-228.
- JUNGE C.E. (1958) The distribution of Ammonia and Nitrate in rainwater over the United States.  
Trans. Am. Geophys. Union. 39 241-248.
- KING P.J. (1962) Personal communication.
- KITSON R.E., MELLON M.G. (1944) Colorimetric determination of Phosphorus as Molybdovanadophosphoric acid.  
Industr. & Eng. Chem. (Anal. Edn.) 16 379. (Now Analyt. Chem.)

- LAWRENCE D.B. (1941) The "Floating Island" lava flow of Mt. St. Helens.  
Mazama 23 56-60.
- LAWRENCE D.B. (1950) Estimating dates of recent glacier advances and recession rates by studying the tree growth layers.  
Am. Geophys. Union. Trans. 31 243-248.
- LAWRENCE D.B. (1951a) Glacier fluctuation in North West America within the past six centuries.  
Union Geodesique et Geophysique Internationale 161-165.
- LAWRENCE D.B. (1951b) Recent glacier history of Glacier Bay, Alaska; and development of vegetation and glaciated terrain with special reference to the importance of Alder in the succession.  
Am. Phil. Soc. Yrbk. 1950 175-176.
- LAWRENCE D.B. (1953) Development of vegetation and soil in South East Alaska, with special reference to the accumulation of Nitrogen.  
Final report.. ONR Project NR 160-183. (Original not seen)
- LAWRENCE D.B. (1954) Diagrammatic history of the North East slope of Mt. St. Helens, Washington.  
Mazama 36 41-44.
- LAWRENCE D.B. (1958a) Glacier fluctuation for six centuries in South East Alaska, and its relation to solar activity.  
Geogr. Rev. 40 191-223.
- LAWRENCE D.B. (1958b) Glaciers and vegetation in South Eastern Alaska.  
American Scientist. 46 88-122.
- LAWRENCE D.B., ELSON J.A. (1953)  
Periodicity of deglaciation in North America since the late Wisconsin maximum.  
Geogr. Ann. Stockh. 35 83-104.
- LAWRENCE D.B., HULBERT L. (1950)  
Growth stimulation of adjacent plants by lupin and alder on recent glacier deposits in South East Alaska.  
Bull. Ecol. Soc. Am. 31 58.

- LAWRENCE D.B., LAWRENCE E.G. (1959a)  
Recent glacier variations in Southern South America.  
Technical report: Office of Naval Research. ONR 641(04).
- LAWRENCE D.B., LAWRENCE E.G. (1959b)  
Radiocarbon dating of some events on Mt.Hood and Mt. St. Helens.  
Mazama 41 10-18.
- LILLIE A.R., GUNN B.M., ROBINSON P. (1957)  
Structural observations in the central Alpine region of New Zealand.  
T. Roy. Soc. N.Z. 85 (1) 113-129
- LILLIE A.R., MASON B.H. (1954)  
Geological reconnaissance of the district between Franz Josef and the Copland Valley.  
T. Roy. Soc. N.Z. 82 (5) 1123-1128.
- LIPMAA T. (1940) A contribution to the ecology of the Estonian deciduous forest.  
Ann. Acad. Sci. Estonicae. 1 30-85 (original not seen.)
- LUDECKE T.E. (1962) The Soil Chemistry of some Central Otago soils in relation to the pattern of field responses to Sulphur and Phosphorus.  
Thesis: M.Agric. Sci. Deposited at Lincoln College.
- LUDI W. (1945) Beisedelung und Vegetationsentwicklung auf den jungen Seiten moränen des grossen Aletschgletschers.  
Geob. Forsch. Inst. 1944 35-112  
(Original not seen.)
- LUTZ H.J. (1930) Observations on the invasion of newly formed glacial moraines by trees.  
Ecol. 11 562-567.
- MACKNEY D. (1961) A podzol development sequence in Oakwoods and Heath in Central England.  
J. Soil Sci. 12 23-40.
- MAJOR J. (1951) A functional, factorial approach to plant Ecology.  
Ecol. 32 392-412.
- MASTERS S.E., HOLLOWAY J.T., McKELVEY P.J. (1955).  
The National Forest Survey of New Zealand.  
I. The indigenous forest resources of New Zealand.  
N.Z. Government Printer.



- MATTHES F.E. (1945) The American Committee on Glaciers  
(F.E. Matthes, Chairman).  
Nature 158 107. (Refer also to  
Amer. Geophys. Union Trans. 27.)
- McCASKILL M. (1962) "Land and Livelihood" - A collection of  
essays to honour Prof. George Jobberns.  
N.Z. Geographical Soc. Misc.  
Series 4. Christchurch. pp. 280.
- McCORMACK P. (1961) Personal communication.
- METSON A.J. (1956) Methods of Chemical analysis for soil  
survey samples.  
Soil Bureau Bull. 12. N.Z. Dept.  
Sci. Ind. Res.
- MILLER N.H.J. (1906) The amounts of Nitrogen as Ammonia and  
Nitric acid, and of Chlorine in the  
rainwater collected at Rothamsted.  
J. Agric. Sci. 1 280-303.
- Miller R.B. (1961) The chemical composition of rainwater at  
Taita, New Zealand. 1956-1958.  
N.Z. J. Sci. 4 (4) 844-853.
- MOLLOY B.J. (1962) Personal communication.
- MONSI M., OSHIMA Y. (1955)  
A theoretical analysis of the succession  
process, based upon the production of matter.  
Jap. J. Bot. 15 60-82.
- MORRISON T.M. (1957) Host-endophyte relationships in mycorrhizas  
of Pernettya macrostigma.  
New Phytol. 56 247-257.
- MORRISON T.M. (1962) Personal communication.
- MORRISON T.M., HARRIS G.P. (1958)  
Root nodules of Discaria toumatou Raoul  
Choix.  
Nature 182 1746.
- MOUAT M., WALKER T.W. (1959a, 1959b)  
Competition for nutrients between grasses  
and white clover.  
I. Effect of grass species and Nitrogen  
supply.  
II. Effect of root cation exchange capacity  
and rate of emergence of associated species.  
Plant and Soil 11 I. 30-40  
II. 41-52

## NEW ZEALAND GEOLOGICAL SURVEY (1958)

Geological map of New Zealand. 1958.  
Dept. Sci. Ind. Res.

NORDMEYER A.H. (1962) Personal communication.

ODELL N.E. (1955) The Franz Josef Glacier, speed of flow - a small note.  
J. Glaciol. 2 (18) 593.

ODELL N.E. (1960) The mountains and glaciers of New Zealand.  
J. Glaciol. 3 (28) 739-742.

OLSEN J.S. (1958) Rates of succession and soil changes on Southern Lake Michigan sand-dunes.  
Bot. Gaz. 119 125-170.

ONTHANK D.G. (1951) Forest development following glacier recession observed in 1776.  
Ecol. 32 730-731.

OZANNE P.G., KIRTON D.J., SHAW T.C. (1961)  
The loss of Phosphorus from sandy soils.  
Aust. J. Ag. Res. 12 (3) 409-423.

PALMER W.H., MILLER A.K. (1961)  
Botanical evidence for the recession of a glacier.  
Oikos 12 (1) 75-86.

PARKER C.A. (1955) Non-symbiotic Nitrogen fixing bacteria in soil.  
II. Studies on Azotobacter.  
Aust. J. Ag. Res. 6 388-397.

PEARSON M.C., ROGERS J.A. (1962)  
Hippophae rhamnoides L.  
J. Ecol. 50 (2) 501-513.

QUISPEL A. (1954) Symbiotic Nitrogen fixation in non-leguminous plants.  
I. Preliminary experiments on the root nodule symbiosis of Alnus glutinosa.  
II. The influence of the inoculation density and external factors on the nodulation of Alnus glutinosa and its importance to our understanding of the mechanism of the infection.  
Acta. Bot. Neerlandica.  
3 I.. 495-511  
II. 512-532.

- QUISPTEL A. (1955) Symbiotic Nitrogen fixation in non-leguminous plants.  
III. Experiments on the growth in vitro of the endophyte of Alnus glutinosa.  
Acta Bot. Neerlandica. 4. III. 671-689.
- QUISPTEL A. (1960) Acta Bot. Neerlandica 9. 380  
(Original not seen.)
- RAGGIO M., RAGGIO Nora (1962) Root nodules.  
Ann. Rev. Plant Physio. 13 109-128.
- RICHARDSON H.L. (1938) The Nitrogen cycle in grassland soils with particular reference to the Rothamsted Park Grass experiment.  
J. Agric. Sci. 28 73-121.
- SALISBURY E.J. (1925) Note on the edaphic succession in some dune soils with special reference to the time factor.  
J. Ecol. 13 322-328.
- SCHEFFER F., KLOKE A., HEMPLER K. (1960) The forms of Phosphorus in soil and their distribution between the particle-size fractions.  
Z. Pflernahr. Dung. 91 240-252.  
(Abstract only seen.)
- SCHOENICKE R.E. (1957-58) Influence of Mountain avens (Dryas Drummondii) on growth of young Cottonwoods (Populus trichocarpa) at Glacier Bay, Alaska.  
Proc. Minn. Acad. Sci. 25-26. 55-58.
- SCOTT G.D. (1956) Further investigation of some lichens for fixation of Nitrogen.  
New Phytol. 55 111-116.
- SJORS H. (1955) Remarks on ecosystems.  
Svens. Bot. Tids. 49 155-169.
- SPEIGHT R. (1914) Recent changes in the position of the terminal face of the Franz Josef Glacier.  
T. N.Z. Inst. (now Roy. Soc. N.Z.) 47 353-354.

- SPEIGHT R. (1921) Recent changes in the terminal face of the Franz Josef Glacier.  
T. N.Z. Inst. (now Roy. Soc. N.Z.)  
53 53-57.
- SPEIGHT R. (1934) Notes on the Franz Josef Glacier.  
T. Roy Soc. N.Z. 64 315-322.
- SPEIGHT R. (1940a) Note on the Franz Josef Glacier.  
T. Roy. Soc. N.Z. 71 128-133.
- SPEIGHT R. (1940b) Ice wasting and glacier retreat in New Zealand.  
J. Geomorph. 3 131-143.
- STEPHENS C.G. (1947) Functional synthesis in pedology.  
T. Roy. Soc. S. Aust. 71 (2)  
168-181.
- STEPHENS C.G. (1951) The present state of soil science.  
Aust. J. Ag. Res. 17 126-131.
- STEVENSON Greta B. (1953)  
Bacterial symbiosis in some New Zealand plants.  
Ann. Bot. Lond. NS 17 343-346.
- STEVENSON Greta B. (1957)  
Nitrogen fixation by higher plants.  
Soil News. 1957 (2) 40.
- STEVENSON Greta B. (1958)  
Use of N<sub>15</sub> in the study of fixation of atmospheric Nitrogen by non-nodulated seed plants.  
Proc. 2nd United Nations Conf. on the Peaceful Uses of Atomic Energy. Geneva. 27 51-56.
- STEVENSON Greta B. (1959)  
Fixation of Nitrogen by non-nodulated seed plants.  
Ann. Bot. Lond. NS 23 622-635.
- SUGGATE R.P. (1949) Franz Josef and the other glaciers of the Southern Alps in New Zealand.  
J. Glaciol. 1 (8) 422-429.
- SUGGATE R.P. (1951) Franz Josef Glacier.  
N.Z. J. Sci. Tech. 33B 299-304.

- TANSLEY A.G. (1929) Succession; the concept and its values.  
Proc. Int. Cong. Plant. Sci. (1926)  
677-686.
- TANSLEY A.G. (1935) The uses and abuses of vegetational concepts  
and terms.  
Ecol. 16 284-307.
- TANSLEY A.G. (1954) "Introduction to Plant Ecology"  
London.
- TAYLOR N.H., et al (1948)  
The Soil Map of New Zealand. 1948.  
N.Z. Dept. Sci. Ind. Res. Soil  
Bureau.
- TAYLOR N.H., COX J.E. (1956)  
The Soil Pattern of New Zealand.  
Proc. N.Z. Inst. Ag. Sci. 28 44.
- TAYLOR N.H., POHLEN I.J. (1962)  
"Soil Survey Method" - A New Zealand  
Handbook for the Field Study of Soils.  
Soil Bureau Bull. 25 N.Z. Dept.  
Sci. Ind. Res.
- TCHAN Y.T., BEADLE N.C.W. (1955)  
Nitrogen economy in semi-arid plant  
communities.  
II. The non-symbiotic Nitrogen fixing  
organisms.  
Proc. Linn. Soc. N.S.W. 80 (2)  
97-104.
- TEZUKA Yasuhiko (1958)  
On the relationship between plant growth  
and Nitrogen supply under water culture  
conditions. Relations of plant communities  
to edaphic factors with special reference  
to mineral nutrition.  
Bot. Mag. 71 181-186.
- TEZUKA Yasuhiko (1961)  
Development of vegetation in relation to  
soil formation in the volcanic island of  
Oshima, Izu, Japan.  
Jap. J. Bot. 17 (3) 371-402.
- VIRTANEN A.I. (1952) Molecular Nitrogen fixation and the  
Nitrogen cycle in Nature.  
Tellus 4 304-306.
- von HAAST J. (1879) "Geology of Canterbury and Westland".  
Published by "Times", Christchurch.

- WALKER T.W. (1956a) The accumulation of organic matter in grassland soils.  
Trans. 6th Int. Cong. Soil Sci. 409-416.
- WALKER T.W. (1956b) Nitrogen and herbage production.  
Proc. 7th Int. Grassl. Cong. 157-167.
- WALKER T.W. (1956c) The Nitrogen cycle in grassland soils.  
J. Sci. Food Agric. 7 67-72.
- WALKER T.W. (1962) Problems of soil fertility in a grass animal regime.  
1962 Int. Cong. Soil Sci. (In press)
- WALKER T.W., ADAMS A.F.R. (1958)  
Studies on soil organic matter.  
I.. Influence of Phosphorus content of parent materials on accumulations of Carbon, Nitrogen, Sulphur and organic Phosphorus in grassland soils.  
Soil Sci. 85 307-318.
- WALKER T.W., ADAMS A.F.R. (1959)  
Studies on soil organic matter.  
II. Influence of increased leaching at various stages of weathering on levels of Carbon, Nitrogen, Sulphur and organic and inorganic Phosphorus.  
Soil Sci. 87 1-10.
- WALKER T.W., ORCHISTON H.D., ADAMS A.F.R. (1954)  
The Nitrogen economy of grass-legume associations.  
J. Brit. Grassl. Soc. 9 249-274.
- WALKER T.W., THAPA B.K., ADAMS A.F.R. (1959)  
Studies on soil organic matter.  
III. Accumulation of Carbon, Nitrogen, Sulphur and organic and inorganic Phosphorus in improved grassland soils.  
Soil Sci. 87 135-140.
- WALL A. (1925) "The Flora of Mount Cook."  
Lyttelton Times Company, Ltd.  
Christchurch. pp.55.
- WARD W.T. (1958) "K cycles", groundsurfaces and the time dimension in pedology.  
Soil News 1958 (6) 105-108.
- WARDLE P. (1962) Personal communication.

- WELLMAN H.W. (1956) Structural outline of New Zealand.  
Dept. Sci. Ind. Res. N.Z. Bull. 121.
- WELLMAN H.W., WILLETT R.W. (1941)  
The geology of the West Coast from Abut  
Head to Milford Sound. Parts I, II.  
I. T. Roy. Soc. N.Z. 71 282-306.  
II. T. Roy. Soc. N.Z. 72 199-219.
- WILDE S.A., VOIGT G.K., PIERCE R.S. (1954)  
The relationship of soils and forest growth  
in the Algoma district of Ontario, Canada.  
J. Soil Sci. 5 22-38.
- WILLETT R.W. (1950) The New Zealand Pleistocene snow-line,  
climatic conditions and suggested  
biological effects.  
N.Z. J. Sci. Tech. 32B (1) 18-48.
- WILLIAMS E.G., SAUNDERS W.M.H. (1956a)  
Distribution of Phosphorus in profiles and  
particle-size fractions of some Scottish  
soils.  
J. Soil Sci. 7 90-108.
- WILLIAMS E.G., SAUNDERS W.M.H. (1956b)  
Significance of particle-size fractions in  
readily soluble Phosphorus extractions by  
the acetic, Truog and lactate methods.  
J. Soil Sci. 7 189-202.
- WILLIS A.J., FOLKES B.F., HOPE-SIMPSON J.F., YEMM E.W. (1959)  
Braunton Burrows: the dune system and its  
vegetation. Parts I and II.  
J. Ecol. 47 I. 1-24  
II. 249-288.
- WILSON A.T. (1959a) Organic Nitrogen in New Zealand snows.  
Nature 183 318-319.
- WILSON A.T. (1959b) Surface of the ocean as a source of  
airborne Nitrogenous material and other  
plant nutrients.  
Nature 184 99-101.
- WILSON A.T. (1962) Personal communication.
- WILSON P.W. (1958) Asymbiotic Nitrogen fixation.  
Encycl. Plant Physio. 8 9-47  
Springer-Verlag; Berlin. 1958.

- WRIGHT A.C.S. (1949) The role of biotic surveys in soil studies.  
Proc. 7th Pac. Sci. Cong. VI 29-31.
- WRIGHT A.C.S., MILLER R.B. (1952)  
Soils of South West Fiordland.  
Soil Bureau Bull. 7 NS  
N.Z. Dept. Sci. Ind. Res.
- WRIGHT T.W. (1955)(1956)  
Profile development in the sand-dunes of  
Culbin Forest, Morayshire. Parts I. and II.  
J. Soil Sci. 6 I. 270-283.  
ibid 7 II. 33-42.
- WRIGHT T.W., WILL G.M. (1958)  
The nutrient content of Scots and Corsican  
Pines growing on sand-dunes.  
Forestry. 31 13-25.
- ZACH L.W. (1950) A Northern Climax - Forest or Muskeg?  
Ecol. 31 304-306.
- ZEUNER F.E. (1958) "Dating the Past"  
Methuen and Co. Ltd. 4ed. London.  
pp. 516.



APPENDIX I.The Western South Island Raoulia association, and river-bed forest.

Reproduced from Cockayne (1928) - p.209.

This is distinguished by the absence of many of the Eastern xerophytes and the presence of Mazus radicans, Acaena Sanguisorbae var sericeinitens and species of Coriaria and their numerous, polymorphic hybrids. Frequently the vegetation is closed. Here the association of the Western district is alone considered.

The following are the important species: - Carex comans, Muehlenbeckia axillaris, Ranunculus foliosus (sometimes), Acaena Sanguisorbae var sericeinitens, A. inermis, Coriaria sarmentosa, C. lurida X C. sarlurida, Pimelia prostrata var repens, Epilobium pedunculare, Hydrocotyle novae-zealandiae, Mazus radicans, Veronica lyallii (common in montane belt, but rare at sea-level), Coprosma rugosa, C. brunnea, Nertera depressa, Wahlenbergia albomarginata, Pratia angulata, Helichrysum filicaule, H. bellidioides, Cotula squalida, Raoulia glabra (sometimes), R. australis, R. tenuicaulis.

The station, thanks to the frequent downpour, is mesophytic notwithstanding the coarse, stony substratum. Rocks far larger than on eastern river-bed are present. Hot dry winds are

virtually unknown; frosts are never heavy.

On older river bed shrubs come in, and there is a procession of events leading eventually to forest.

This is distinguished by the close growth of low slender trees and the presence of species wanting or rare in the adjacent lowland forest e.g. Rubus schmidelioides var coloratus, Coriaria arborea, Pennantia corymbosa, Aristotelia serrata, Plagianthus betulinus and Coprosma rotundifolia, as a tree. Here only the association of the Western district receives consideration. The species may be seen from what follows.

The ground is level and traversed by numerous streams. The upper soil consists of humus beneath which is merely river-shingle. The vegetation is in three layers - the floor plants, the small tree-ferns and shrubs, and the low trees. The association is 4.5 to 6 m. high. Slender tree-trunks not exceeding 15 cm. diam. are the rule; they may be erect or more or less leaning and draped with a moss-mantle, while from their branches hangs the pale moss Weymouthia Billardieri. Coprosma rotundifolia, elsewhere usually a shrub, is the dominant tree, and it grows in such profusion at times as to make pure stands. Besides the trees already mentioned, the following are common:- Carpodetus serratus, Melicytus ramiflorus, Fuschia excorticata, Pseudopanax crassifolium var unifoliolatum and Griselinia littoralis. Podocarpus acutifolius and Weinmannia racemosa may occur. The second tier consists of young forest-trees, the Coprosma-form dominating together with small Dicksonia squarrosa

and Hemitelia Smithii and the semi-tree-ferns Polystichum vestitum and Dryopteris pennigera. On the floor are mosses, liverworts, the liane Metrosideros hypericifolia (creeping), Blechnum procerum and B. fluviatile.

The lianes Rubus schmidelioides var coloratus, Metrosideros hypericifolia and Polypodium diversifolium are common, the two latter being especially abundant on tree-fern stems. The filmy ferns, Hymenophyllum scabrum, H. sanguinolentum and Trichomanes reniforme cover the leaning trunks, particularly of Griselinia littoralis. Polypodium grammitidis, P. Billardieri and the orchid Earina mucronata are fairly common as epiphytes.

At an altitude of some 300 m. on river bed in the Western District there is an association closely allied to subalpine totara forest, although that of the adjacent slopes is Weinmannia-Metrosideros and that of the swamps Podocarpus dacrydiodes.

Podocarpus Hallii, Phyllocladus alpinus (a tree) and Pseudopanax crassifolium var unifoliolatum are dominant and Libocedrus Bidwillii sub-dominant. The forest is low, and the trees etc. are erect. The undergrowth consists principally of Polystichum vestitum, Pittosporum divaricatum, Aristotelia fruticosa, Nothopanax simplex, N. anomalum, Suttonia divaricata, Coprosma rotundifolia, C. propinqua, Olearia ilicifolia, O. avicenniaefolia. There is also some Wintera colorata, Carpodetus, Pittosporum Colensoi, Pennantia, Myrtus pedunculata and Griselinia littoralis. Rubus schmidelioides var coloratus is the sole liane.

## APPENDIX II.

### Southern-rata (Metrosideros lucida) forest.

Reproduced from Cockayne (1928) - p. 170.

At the Franz Josef Glacier, the terminal face of which descends to 213 m., the southern-rata association comes onto the ice-worn rocks at a few metres from the ice on either side of the Glacier. The forest here, the roof of which has the characteristic billowy appearance, consists principally of the following:- Metrosideros lucida and Weinmannia racemosa (the dominant canopy trees), Carpodetus serratus, Coriaria arborea, Aristotelia serrata, Hoheria glabrata, Melicytus ramiflorus, Pseudopanax crassifolium var unifoliolatum, Shefflera digitata, Grisellinia littoralis, Hebe salicifolia, Coprosma lucida, Olearia arborescens, O. avicenniaefolia. The pteridophytes include Hemitelia Smithii (tree-fern, but here of low stature), several Hymenophyllaceae, Hypolepis tenuifolia, Histiopteris incisa, Blechnum procerum, B. lanceolatum, Asplenium bulbiferum, A. flaccidum, Polystichum vestitum, Polypodium diversifolium, P. Billardieri, and Lycopodium volubile.

Detailed values for reaction of mineral soil and F/H.

Stage	Pit	Mineral Material		<u>F/H</u>
		Upper Horizon	Lower Horizon	
I	1	7.71	-	-
	2	8.07	-	-
	3	7.88	-	-
II	1	7.57	-	-
	2	7.43	-	-
	3	7.51	-	-
III	1	7.44	-	-
	2	7.19	-	-
	3	7.15	-	-
IV	1	5.76	6.68	5.22
	2	5.54	6.42	5.41
	3	5.54	6.56	5.27
V	1	5.49	6.05	5.63
	2	5.68	6.70	5.39
	3	5.73	6.37	5.50
VI	1	4.96	5.22	5.23
	2	5.45	5.61	5.76
	3	5.45	5.51	5.62

## Detailed values for organic Carbon.

Stage	Pit	Upper Horizon		Lower Horizon		<u>F/H</u>		<u>V</u>		Upper + Lower	Upper + Lower + <u>F/H</u>	Ecosystem
		%C	(g/m <sup>2</sup> )	%C	(g/m <sup>2</sup> )	%C	(g/m <sup>2</sup> )	%C	(g/m <sup>2</sup> )			
I	1	0.13	72	-	-	-	-	-	-	72	72	72
	2	0.15	117	-	-	-	-	-	-	117	117	117
	3	0.13	86	-	-	-	-	-	-	86	86	86
II	1	0.09	120	-	-	-	-	28.66	49	120	120	169
	2	0.11	81	-	-	-	-	8.19	30	81	81	111
	3	0.13	87	-	-	-	-	21.12	27	87	87	114
III	1	0.14	154	-	-	-	-	45.58	269	154	154	423
	2	0.08	60	-	-	-	-	26.62	325	60	60	385
	3	0.20	174	-	-	-	-	37.10	1106	174	174	1280
IV	1	1.36	332	0.42	206	14.32	914	42.42	2528	538	1452	3980
	2	0.97	393	0.21	188	11.50	393	35.36	1379	581	974	2353
	3	0.79	290	0.20	234	11.78	431	39.72	2768	524	955	3723
V	1	4.59	753	0.68	464	26.26	439	40.26	1574	1217	1656	3230
	2	1.80	727	0.50	177	26.93	563	39.06	1246	904	1467	2713
	3	2.31	963	0.43	213	28.52	660	42.00	1457	1176	1836	3293
VI	1	2.57	1236	0.62	538	29.84	871	41.32	1855	1774	2645	4500
	2	3.63	457	0.95	557	31.45	937	41.44	3444	1014	1951	5395
	3	4.32	492	1.11	508	25.85	1285	41.44	5192	1000	2285	7477

Detailed values for Nitrogen.

Stage	Pit	Upper Horizon		Lower Horizon		F/H		V		Upper + Lower	Upper + Lower + F/H	Ecosystem
		%N	(g/m <sup>2</sup> )	%N	(g/m <sup>2</sup> )	%N	(g/m <sup>2</sup> )	%N	(g/m <sup>2</sup> )			
I	1	0.013	7.2	-	-	-	-	-	-	7.2	7.2	7.2
	2	0.014	10.9	-	-	-	-	-	-	10.9	10.9	10.9
	3	0.012	8.0	-	-	-	-	-	-	8.0	8.0	8.0
II	1	0.014	18.6	-	-	-	-	0.364	0.6	18.6	18.6	19.2
	2	0.013	9.6	-	-	-	-	0.190	0.7	9.6	9.6	10.3
	3	0.014	9.4	-	-	-	-	0.445	0.6	9.4	9.4	10.0
III	1	0.016	17.6	-	-	-	-	1.345	7.9	17.6	17.6	25.5
	2	0.016	12.0	-	-	-	-	0.844	10.3	12.0	12.0	22.3
	3	0.024	20.9	-	-	-	-	1.490	44.4	20.9	20.9	65.3
IV	1	0.086	21.0	0.027	13.2	0.743	47.4	1.019	60.7	34.2	81.6	142.3
	2	0.072	29.2	0.027	24.1	0.507	17.3	0.797	31.1	53.3	70.6	101.7
	3	0.050	18.4	0.026	30.5	0.555	20.3	0.765	53.3	48.9	69.2	122.5
V	1	0.305	50.0	0.048	32.8	1.408	23.5	0.592	23.1	82.8	106.3	129.4
	2	0.130	52.5	0.034	12.0	1.571	32.8	1.306	41.7	64.5	97.3	139.0
	3	0.152	63.4	0.029	14.4	1.546	35.6	0.624	21.7	77.8	113.4	135.1
VI	1	0.171	82.3	0.046	39.9	1.418	41.4	0.473	21.2	122.2	163.6	184.8
	2	0.232	29.2	0.060	35.3	1.292	38.5	0.377	31.3	64.5	103.0	134.3
	3	0.262	29.9	0.074	33.9	1.265	62.9	0.497	62.3	63.8	126.7	189.0

Detailed values for total and inorganic Phosphorus  
(Upper and Lower horizons and F/H)

All figures expressed as parts per million.

Stage	Pit	Upper horizon		Lower horizon		Mean of Upper and Lower		<u>F/H</u>	
		P <sub>t</sub>	P <sub>a</sub>	P <sub>t</sub>	P <sub>a</sub>	P <sub>t</sub>	P <sub>a</sub>	P <sub>t</sub>	P <sub>a</sub>
I	1	744	730	-	-	744	730	-	-
	2	738	722	-	-	738	722	-	-
	3	759	741	-	-	759	741	-	-
II	1	681	648	-	-	681	648	-	-
	2	777	731	-	-	777	731	-	-
	3	716	667	-	-	716	667	-	-
III	1	738	691	-	-	738	691	-	-
	2	746	727	-	-	746	727	-	-
	3	752	719	-	-	752	719	-	-
IV	1	695	653	807	774	751	714	905	654
	2	722	632	779	731	751	682	827	507
	3	709	634	735	693	722	664	684	392
V	1	646	565	737	675	692	620	1184	536
	2	764	666	775	749	770	708	1245	559
	3	693	608	745	739	719	674	1103	550
VI	1	610	491	712	693	661	592	1108	459
	2	650	476	724	706	687	591	1096	414
	3	670	583	744	727	707	655	1036	417



# APPENDIX III (e)

Detailed values for total and inorganic Phosphorus.

(Upper and Lower horizons and  $F/H$ )

(All figures expressed as  $g/m^2$ .)

Stage	Pit	Upper horizon		Lower horizon		$F/H$		Upper + Lower + $F/H$	
		$P_t$	$P_a$	$P_t$	$P_a$	$P_t$	$P_a$	$P_t$	$P_a$
I	1	41.44	40.66	-	-	-	-	41.44	40.66
	2	57.49	56.24	-	-	-	-	57.49	56.24
	3	50.32	49.13	-	-	-	-	50.32	49.13
II	1	90.50	86.12	-	-	-	-	90.50	86.12
	2	57.26	53.87	-	-	-	-	57.26	53.87
	3	48.12	44.82	-	-	-	-	48.12	44.82
III	1	81.18	76.01	-	-	-	-	81.18	76.01
	2	55.88	54.45	-	-	-	-	55.88	54.45
	3	65.57	62.70	-	-	-	-	65.57	62.70
IV	1	16.96	15.93	39.54	37.93	5.77	4.17	62.27	58.03
	2	29.24	25.60	69.64	65.35	2.83	1.73	101.71	92.68
	3	26.02	23.27	86.14	81.22	2.50	1.43	114.66	105.92
V	1	10.59	9.27	50.34	46.10	1.98	0.90	62.91	56.27
	2	30.87	26.91	27.36	26.44	2.60	1.17	60.83	54.52
	3	28.90	25.35	36.95	36.65	2.54	1.27	68.39	63.27
VI	1	29.34	23.62	61.80	60.15	3.24	1.34	94.38	85.11
	2	8.19	6.00	42.57	41.51	3.27	1.23	54.03	48.74
	3	7.64	6.65	34.08	33.30	5.15	2.07	46.87	42.02

Detailed values for organic Phosphorus.

(All figures expressed as  $\text{g/m}^2$ )

Stage	Pit	Upper Horizon	Lower Horizon	F/H	<u>Y</u>		Upper + Lower		Upper + Lower + <u>F/H</u>		Ecosystem	
					%P	( $\text{g/m}^2$ )		%P <sub>O</sub> of P <sub>t</sub>		%P <sub>O</sub> of P <sub>t</sub>		%P <sub>O</sub> of P <sub>t</sub>
I	1	0.78	-	-	-	-	0.78	1.9	0.78	1.9	0.78	1.9
	2	1.25	-	-	-	-	1.25	2.2	1.25	2.2	1.25	2.2
	3	1.19	-	-	-	-	1.19	2.4	1.19	2.4	1.19	2.4
II	1	4.38	-	-	0.082	0.14	4.38	4.8	4.38	4.8	4.52	5.0
	2	3.39	-	-	0.059	0.22	3.39	5.9	3.39	5.9	3.61	6.3
	3	3.30	-	-	0.062	0.08	3.30	6.9	3.30	6.9	3.38	7.0
III	1	5.17	-	-	0.053	0.31	5.17	6.4	5.17	6.4	5.48	6.7
	2	1.43	-	-	0.071	0.87	1.43	2.6	1.43	2.6	2.30	4.1
	3	2.87	-	-	0.081	2.42	2.87	4.4	2.87	4.4	5.29	7.8
IV	1	1.03	1.61	1.60	0.053	3.16	2.64	4.7	4.24	6.8	7.40	11.3
	2	3.64	4.29	1.10	0.079	3.07	7.93	8.0	9.03	8.9	12.10	11.6
	3	2.75	4.92	1.07	0.067	4.68	7.67	6.8	8.74	7.6	13.42	11.2
V	1	1.32	4.24	1.08	0.043	1.68	5.56	9.1	6.64	10.6	8.32	12.9
	2	3.96	0.92	1.43	0.069	2.19	4.88	8.4	6.31	10.4	8.50	13.5
	3	3.55	0.30	1.27	0.031	1.07	3.85	5.8	5.12	7.5	6.19	8.9
VI	1	5.72	1.65	1.90	0.039	1.77	7.37	8.1	9.27	9.8	11.04	11.5
	2	2.19	1.06	2.04	0.039	3.27	3.25	6.4	5.29	9.8	8.56	14.9
	3	0.99	0.78	3.08	0.027	3.42	1.77	4.2	4.85	10.3	8.27	16.4

APPENDIX III (g)

Detailed values for nutrient ratios.

(Calculated on g/m<sup>2</sup> of nutrients as in previous tables.)

Stage	Pit	Upper Horizon			Lower Horizon			<u>F/H</u>			<u>V</u>			Upper + Lower			Upper + Lower + <u>F/H</u>			Ecosystem		
		C/N	C/P <sub>o</sub>	N/P <sub>o</sub>	C/N	C/P <sub>o</sub>	N/P <sub>o</sub>	C/N	C/P <sub>o</sub>	N/P <sub>o</sub>	C/N	C/P <sub>o</sub>	N/P <sub>o</sub>	C/N	C/P <sub>o</sub>	N/P <sub>o</sub>	C/N	C/P <sub>o</sub>	N/P <sub>o</sub>	C/N	C/P <sub>o</sub>	N/P <sub>o</sub>
I	1	10.0	92	9.2	-	-	-	-	-	-	-	-	-	10.0	92	9.2	10.0	92	9.2	10.0	92	9.2
	2	10.7	94	8.7	-	-	-	-	-	-	-	-	-	10.7	94	8.7	10.7	94	8.7	10.7	94	8.7
	3	10.8	72	6.7	-	-	-	-	-	-	-	-	-	10.8	72	6.7	10.8	72	6.7	10.8	72	6.7
II	1	6.5	27	4.3	-	-	-	-	-	-	81.7	350	4.3	6.5	27	4.3	6.5	27	4.3	8.8	38	4.2
	2	8.4	24	2.8	-	-	-	-	-	-	42.9	136	3.2	8.4	24	2.8	8.4	24	2.8	10.8	31	2.9
	3	9.3	26	2.8	-	-	-	-	-	-	45.0	338	7.5	9.3	26	2.8	9.3	26	2.8	11.4	34	3.0
III	1	8.8	30	3.4	-	-	-	-	-	-	34.1	868	25.5	8.8	30	3.4	8.8	30	3.4	16.6	77	4.7
	2	5.0	42	8.4	-	-	-	-	-	-	31.6	374	11.8	5.0	42	8.4	5.0	42	8.4	17.3	167	9.7
	3	8.3	61	7.3	-	-	-	-	-	-	24.9	457	18.3	8.3	61	7.3	8.3	61	7.3	19.6	242	12.3
IV	1	15.8	322	20.4	15.6	128	8.2	19.3	571	29.6	41.6	800	19.2	15.7	204	13.0	17.8	343	19.2	28.0	538	19.2
	2	13.5	108	8.0	7.8	44	5.6	22.7	357	15.7	44.3	449	10.1	10.9	73	6.7	13.8	108	7.8	23.1	195	8.4
	3	15.8	106	6.7	7.7	48	6.2	21.2	403	19.0	51.9	592	11.4	10.7	68	6.4	13.8	109	7.9	30.4	277	9.1
V	1	15.1	571	37.9	14.1	109	7.7	18.7	407	21.8	68.1	937	13.8	14.7	219	15.0	15.6	249	16.0	25.0	388	15.6
	2	13.9	184	13.3	14.8	192	13.0	17.2	394	22.9	29.9	569	19.0	14.0	185	13.2	15.1	233	15.4	19.5	319	16.4
	3	15.2	271	17.9	14.8	710	48.0	18.5	520	28.0	67.1	1362	20.3	15.1	306	20.2	16.2	359	22.1	24.4	532	21.8
VI	1	15.0	216	14.4	13.5	326	24.2	21.0	458	21.8	87.5	1048	12.0	14.5	241	16.6	16.2	285	17.6	24.4	408	16.7
	2	15.7	209	13.3	15.8	526	33.3	24.3	459	18.9	110.0	1053	9.6	15.7	312	19.8	18.9	369	19.5	40.2	630	15.7
	3	16.5	497	30.2	15.0	651	43.5	20.4	417	20.4	83.3	1518	18.2	15.6	565	36.0	18.0	471	26.1	39.6	904	22.9

#### APPENDIX IV.

Reproduced below is an adaption of a letter from Dr M. di Menna, of the Soil Bureau, Lower Hutt, to Professor T.W. Walker, embodying the results of microbiological analyses of some preliminary samples collected from Franz Josef during December, 1962. They are of definite indirect interest, as they provide further evidence of the conditions existing in the sequence of soils from bare ground to heavily afforested and well-developed soils. "Litter" here refers to F/H.

#### Yeasts.

Stage I. 50 - 200 cells/g.; predominantly Candida scottii and Candida tropicalis, with some isolates of common species from plant leaves, which can be regarded as contaminants.

Stages II and III, also Stage intermediate between I and II. No yeasts isolated, or only occasional colonies. All isolates are contaminant species from leaves.

Stage IV. 5,000 - 42,000 cells/g.; 40% Cryptococcus albidus, 45% Candida humicola, 10% Candida curvata.

Stage X. Litter: 14,000 - 100,000 cells/g.; 80% Candida curvata, 15% Cryptococcus albidus.

Stage X. Mineral soil: 4,000 - 16,000 cells/g.; 60% Candida curvata, 25% Candida humicola, 15% Cryptococcus albidus.

The yeast isolates from Stage I suggest that there is a true, if scanty, yeast flora there; it will probably be limited to those parts of Stage I washed by melt-water. Candida scottii

is common in Antarctic soils; Candida tropicalis, in spite of its name, seems to occur most frequently in Sub-Antarctic and alpine soils.

Lack of yeast flora in Stages II and III may be attributable to very sharp drainage and consequent periods of drought, even if infrequent.

By Stage IV, accumulation of humus has improved the water holding capacity of the soil to a point at which yeasts can establish themselves, but predominant species are ones resistant to desiccation.

At "Stage X" water retention has again improved so that Candida curvata, which cannot resist desiccation, is dominant. The species pattern in this soil is very similar to that in the "Okarito", but numbers are much higher. The low count in "Okarito" soil has been attributed to the higher water table and poor aeration. Apparently at "Stage X" drainage is still good enough to prevent low oxygen tensions from being a limiting factor for yeasts. I am tempted to regard the litter layer as top-soil, mineral soil as the sub-soil.

#### Free-living Nitrogen-fixing bacteria.

Neither Azotobacter nor Beijerinckia could be recovered from any of the soil samples from Stages I, II, III, IV and "X" (Litter and Soil), nor from the Stage intermediate between I and II. Dilutions as low as one-tenth were used. Nitrogen-fixing Clostridia were recovered as follows:

Stage I. 10 cells/g. in one of three samples, none in other two.

Intermediate Stage between I and II. 10 cells/g. in two samples,  
100 cells/g. in the third.

Stage II. 10 cells/g. in one of three samples, none in other two.

Stage III. 100 cells/g. in one sample, 10 cells/g. in a second,  
none in the third.

Stage IV. None found.

Stage X. Litter: none found.

Soil: 100 cells/g. in one sample, 10 cells/g. in  
other two.

Jensen's method for isolation of Clostridia was used.

When followed through in culture the organisms appear to grow anaerobically in a Nitrogen-free medium. The paucity of free-living Nitrogen-fixers is most interesting in the light of the type of vegetation colonising the Franz Josef sequence.

## APPENDIX V.

The following notes are adapted from some preliminary observations on algae in the soils near the Franz Josef Glacier, supplied by Dr. E.A. Flint, whose interest, and permission to publish these results, is gratefully acknowledged.

Although algae were present at each Stage in the development of the soils, their distribution was not uniform throughout the sequence. It is not only the species themselves which vary, but also the habitats they occupy. Most of the algae occurred as free-living (non-symbiotic) organisms - on bare rock (Trentepohlia iolithus), on the surface of the soil (Hormidium spp.), or as epiphytes on the leaves of mosses (Mesotaenium spp., Nostoc spp.). In addition to this group there was a smaller one consisting of symbiotic species, such as Trebouxia (an algal component of lichens) and Nostoc punctiforme (?) (endophytic in the nodes of *Gunnera albocarpa*).

A provisional list of the algae so far recorded is given in Table 1. Relatively few species were isolated from samples of Stage I, more were found in Stage II, the maximum number occurred in Stages III and IV, and very few were seen in soils from Stages V and VI.

Each of the communities is dominated by species of Green algae; a few Blue-green algae occurred in Stages II - VI. Regarding the occurrence of diatoms; it is interesting that diatoms which are usually regarded as typical of soil did not

appear in the sequence until Stage IV, apart from the few found in Stage I (probably aquatic forms). The absence of diatoms from Stage III is surprising and needs confirming. One diatom was recorded in Stage V, but none on Stage VI.

A conspicuous feature of the landscape just below the terminal moraine is the patches of Trentepohlia iolithus, growing on the horizontal and vertical faces of otherwise bare rock. It is essentially a terrestrial alga which is distributed by wind and rain, and which may survive periods of desiccation. It may be regarded as an important pioneer on stable rock, persisting in such places into Stages II and III. The appearance of higher plants in the soil sequence provides some habitats for terrestrial algae and the risk of desiccation is reduced, but the growth of Coriara and Olearia (as in Stage IV) and the presence of leaf litter reduce the illumination at the surface of the soil. It has been found elsewhere that relatively few algae (and these are usually species of Green algae) occur on litter-covered soils. This may explain the poor growth of algae in Stages V and VI.

All the Blue-green algae and several of the Green algae (particularly some of those in Stages II and III) form mucilaginous envelopes, which reduce the amount of desiccation that the cells may undergo.

With regard to the contribution the Blue-green algae may make to the Nitrogen content of the soil; it is known that in the absence of combined Nitrogen and under alkaline conditions



several species of Nostoc can fix atmospheric Nitrogen, and it has been found that several Blue-green algae excrete extracellular nitrogenous substances into the medium in which they are growing (Fogg. G.E., 1956; Ann. Rev. Plant Physiol. 7, 51-70). Although Blue-green algae were not abundant at any Stage (it is not yet known if they are the algal components of any of the lichens in the area), it is unfortunate that neither the species of the free-living Nostoc nor the species growing in Gunnera have been identified yet. It is possible that the species of Nostoc present in Stages II, III and IV are N-fixing; and that, together with other Blue-green algae which excrete nitrogenous extracellular substances, they may contribute to the Nitrogen content of the soils.

In general, the algal communities appear to be more important during the early Stages of soil development, when the sub-stratum is alkaline and before it is covered with leaf-litter.

Table 1.. Occurrence of Algae in Stages of the Chronosequence.

GENERA.	STAGES...	I.	II.	III.	IV.	V.	VI.
<u>Green algae.</u>							
Ankistrodesmus spp.		.	+	.	+	.	.
Bracteacoccus spp.		+	+	.	.	.	.
Chlorella spp.		.	+	.	.	.	+
Coccomyxa spp.		.	+	.	+	+	+
Cylindrocystis spp.		.	.	.	+	.	.
Euastrum decedens		.	.	.	+	.	.
Gleocystis spp.		.	+	+	.	.	.
Gongrosira spp.		.	.	+	.	.	.
Hormidium spp.		.	+	+	+	.	.
Mesotaenium spp.		.	.	+	.	.	.
Rhopalocystis spp.		.	.	+	+	.	.
Spongiochloris spp.		.	.	+	.	.	.
Stichococcus spp.		+	.	+	.	+	.
Trebouxia spp.		.	.	+	.	.	.
Trentepohlia iolithus		+	+	+	.	.	.

Blue-green algae.

Microcoleus spp.	.	+	+	+	+	+
Nostoc spp.	.	+	+	+	.	.
Nostoc punctiforme (?) (in <u>Gunnera</u> )	.	+	+	.	.	.
Stigonema spp.	.	.	+	.	.	.

Diatoms.

Eunotia spp.	.	.	.	+	.	.
Hantzschia amphioxys	.	.	.	+	.	.
Pinnularia borealis	.	.	.	+	.	.
Navicula "a"	+	.	.	.	.	.
"b"	.	.	.	+	.	.
"c"	.	.	.	.	+	.
Fragilaria spp. (?)	+	.	.	.	.	.